Investigating the Impacts of Multiple Stressors on Marine Coastal Ecosystems

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Declaration

I declare that this thesis was composed by myself and that the work contained herein is my own except where explicitly stated in the text. The work has not been submitted for any degree or professional qualification except as specified.

Ramesh Wilson, Michaelmas 2025/26

Acknowledgements

Submitting this thesis is the clearest declaration I have of how far I have come, in spite of a difficult life up to this point. As a teenager, I experienced detriment and disappointment beyond what was even comprehensible, all of which made a long and fulfilling life practically unattainable. Somehow, despite numerous setbacks, I made it to university, and receiving a place at Oxford for a DPhil still feels surreal. Over the last four years I have done everything I could to grow into that opportunity, and to earn it in the way I hoped I would.

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I don't need you to sell me on reasons to want you.

I don't need you to search for the proof that I should.

You don't have to convince me.

You don't have to be scared you're not enough.

'Cause what we've got going is good.

I don't need more reminders of all that's been broken.

I don't need you to fix what I'd rather forget.

Clear the slate and start over.

Try to quiet the noises in your head.

We can't compete with all that.

So, what if it's us?

What if it's us and only us.

And what came before won't count anymore or matter?

Can we try that?

What if it's you? And what if it's me?

And what if that's all that we need it to be.

And the rest of the world falls away?

What do you say?

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Abstract

Coastal ecosystems are increasingly exposed to stressors across space and time, including global climate change and local pressures such as nutrient enrichment, pollutants, and habitat modification. Management and cumulative effects assessment often treat combined stressor effects as additive, despite growing recognition of interactive, context-dependent outcomes. This thesis couples *in situ* multiple stressor field experiments with decision-ready governance frameworks for coastal management. Using a passive warming manipulation (black versus white settlement plates) paired with local nutrient enrichment contrasts, Chapter 3 tests independent and interactive stressor impacts on a UK rocky shore through a summer time series and across multiple levels of biological organisation, from genes to populations. Responses span key invertebrate and algal functional groups, alongside trophic and transcriptomic indicators. Enrichment generally increased abundance and cover, whereas warming tended to depress them, and interaction signals were time-structured, most evident for barnacle abundance and cyanobacteria concentration, with synergistic interactions across individual dates and season-wide trends. Chapter 4 applies the same methodology across 22 international sites to estimate global mean effects and quantify cross-site heterogeneity. At the global scale, enrichment increased macroalgal cover and shifted barnacle abundance, while warming reduced both groups. Meta-regressions relate site-level sensitivities to abiotic covariates such as precipitation and air temperature variability, and path analyses indicate that macroalgae mediate a substantial component of indirect stressor effects across ecological communities. Building on this evidence of temporospatial context dependence and wider syntheses, Chapter 5 addresses the policy gap that multiple stressor science is rarely embedded in marine spatial planning and cumulative assessment. It proposes an eight-component management framework integrating land–sea connectivity, blue economy trade-offs, stressor interaction logic, and adaptive monitoring triggers, operationalised through a Massachusetts case study. Collectively, the thesis shows how the context dependence of coastal multiple stressor impacts can be practically interpreted for transparent, adaptive, multi-sectoral governance across the science–policy interface.

1

Introduction

Chapter 1 | Introduction

Marine coastal ecosystems sit at the land–sea interface where biodiversity, productivity, and human uses collide. These systems, including mangroves, seagrass meadows, estuaries, and intertidal shorelines, generate disproportionate ecological and socioeconomic value via primary production, nutrient cycling, habitat provision, shoreline protection, and blue carbon storage, while sustaining numerous coastal livelihoods across fisheries, aquaculture, recreation, and cultural services (Barbier, 2012; Duarte et al., 2013; Fourqurean et al., 2012). The value of these services is vast and well documented across multiple coastal ecosystem types (Barbier, 2012).

Coastal zones now experience an unprecedented combination of synchronous human-driven pressures. Global-scale climate stressors such as ocean warming, acidification, sea-level rise, and increasingly frequent, intense marine heatwaves now interact with growing local and regional stressors such as eutrophication, chemical contamination, sedimentation, overfishing, habitat modification, and invasive species (Breitburg et al., 2018; Doney et al., 2012; Halpern et al., 2008; He & Silliman, 2019; Intergovernmental Panel on Climate Change (IPCC), 2019; Smale et al., 2019). These drivers increasingly co-occur in space and time,

creating exposure scenarios that differ fundamentally from the single-stressor conditions traditionally studied (Halpern et al., 2008; Intergovernmental Panel on Climate Change (IPCC), 2019). In many coastal settings, climate extremes are now a decisive modulator of ecological outcomes, with warming in particular restructuring communities and degrading ecosystem services across numerous basins (Smale et al., 2019).

A central insight from the last two decades is that stressors rarely act independently. Their combined effects can be broadly considered as synergistic, antagonistic, or statistically additive, and interaction type can flip across contexts, scales, taxa, and endpoints (Côté et al., 2016; Crain et al., 2008; Jackson et al., 2021; Orr et al., 2020; Turschwell et al., 2022). This context dependence complicates prediction and management: the same pair of stressors can intensify effects in one setting yet neutralise or reverse each other elsewhere. Compounding these difficulties, both early and contemporary studies may be statistically underpowered or employ null (non-interactive) models unsuited to the scale or transformation of the response, biasing detection of interactions (Burgess et al., 2021, 2022; Duncan & Kefford, 2021). Taken together, contemporary research now encourages robust, factorial designs spanning meaningful gradients, *in situ* realism across spatial and temporal contexts, and clearer bridges from ecological evidence to management frameworks capable of acting on interactive impacts (Intergovernmental Panel on Climate Change (IPCC), 2019; Pirotta et al., 2022).

Intertidal rocky shores are particularly powerful sentinels of change. For instance, because steep tidal and exposure gradients create patchy microclimates, intertidal organisms often reach body temperatures that differ markedly from the surrounding air or water. As a result, even small climatic shifts or brief heatwaves can push them past physiological thresholds, producing disproportionately large biological responses observable at fine spatial and temporal scales (Helmuth et al., 2016). Furthermore, the accessibility and environmental heterogeneity of rocky shores have facilitated the feasibility of *in situ* observations and experimental manipulations that capture realistic species interactions, trophic feedbacks, and variability often missing from *ex situ* designs, thereby improving the external validity of inferences (Hawkins et al., 2020; Pansch & Hiebenthal, 2019; Stewart et al., 2013; Todgham & Stillman, 2013).

Policy and planning have only partially kept pace with the integrated management of multiple stressor impacts. While ecosystem-based management (EBM), integrated coastal zone

management (ICZM), and marine spatial planning (MSP) are now widely promoted both in theory and practice, decision processes still frequently segment issues by sector, stressor, or jurisdiction, leaving interactive effects underspecified at the international convention level, as well as within regional bureaucratic mandates, guidance, and monitoring (Ehler, 2021; Reimer et al., 2023; Zuercher et al., 2022). More recent guidance emphasises enabling conditions for MSP, sociocultural integration, and formal cumulative impact assessments, yet implementation gaps remain at the land–sea interface, where local terrestrial activities drive many marine-associated stressors within a wider context of global change (Frazão Santos et al., 2021, 2024; Pennino et al., 2021; Zuercher et al., 2022).

This thesis advances integrative approaches that couple *in situ* field research with policy analysis and evaluation to interrogate multiple stressor effects across temporal and spatial scales. The following literature review synthesises three themes: 1) the state of knowledge on the value and vulnerability of marine and coastal ecosystems; 2) conceptual and empirical advances in multiple stressor ecology, with emphasis on marine systems; and 3) the current state, and future implications for marine planning and management strategies to address interactive stressor impacts.

2

Literature Review

Chapter 2 | Literature Review

2.1 Coastal ecosystems and anthropogenic stressors

2.1.1 Ecological and environmental importance

Coastal ecosystems rank among the planet's most productive and biodiverse environments, despite occupying less than 5% of Earth's land area (Agardy et al., 2005; Gleason et al., 2023). These dynamic interfaces between land and sea support disproportionately high biodiversity and ecosystem services (Barbier, 2012; Barbier et al., 2011; Barceló et al., 2023; Carlson et al., 2021). Coastal habitats perform critical ecological functions that underpin both marine and terrestrial systems. For example, they facilitate the transfer of nutrients and organic matter across the shoreline, support numerous habitat types (rocky shores, beaches, wetlands, and estuaries) and serve as nursery, foraging, and resting grounds for many species of economic and cultural importance (Beck et al., 2001; Nagelkerken et al., 2015; Preston et al., 2025). Coastal zones act as physical and ecological connectors between marine and terrestrial

biomes, playing a key role in nutrient and sediment flows and buffering human communities from storm surges and sea-level rise (Arkema et al., 2013; Temmerman et al., 2013). Vegetated coastal habitats such as mangrove forests, salt marshes, and seagrass meadows are particularly valuable natural defences; they attenuate wave energy and stabilise shorelines against erosion, trap sediments, and filter runoff (Mazda et al., 1997; Möller et al., 2014; Narayan et al., 2016). Wetland vegetation and substrates act as natural water purifiers, trapping sediments and absorbing pollutants from agricultural and urban runoff, thereby maintaining water quality in rivers, bays, and coastal waters (Barbier et al., 2011; Zedler & Kercher, 2005). By one estimate, coastal wetlands' storm protection services alone avert about US$450 billion globally in storm damage per year, with 4,620 lives saved annually by soaking up floodwaters and slowing storm surges (Costanza et al., 2021). In addition, coastal vegetated habitats sequester significant 'blue carbon', helping regulate the wider climate by storing carbon in plants and sediments (Donato et al., 2011; Fourqurean et al., 2012; McLeod et al., 2011).

The heterogeneous and stressful physical conditions of coasts (e.g. tidal fluxes, salinity gradients, periodic desiccation and inundation, and wave shock) foster high biodiversity by allowing species with specialised adaptations to coexist across multiple microhabitat conditions (Harley et al., 2006; Menge & Sutherland, 1976). For example, combined species- and trait-based surveys in the Baltic Sea quantified taxonomic and functional diversity across rocky shores, including *Fucus* algal belts, seagrass meadows, and bare sand: here, invertebrate richness and trait diversity peaked in seagrass sediments, while fish diversity was highest on bare sand. Furthermore, communities diverged more in species than in traits, with further vegetation-driven structure separating epifaunal from infaunal assemblages (Henseler et al., 2019). This joint taxonomic and trait diversity is facilitated by vegetation and hard substrates that increase structural complexity, enhancing settlement, shelter, and filtering communities along axes such as body size and lifestyle (Henseler et al., 2019). Many coastal species have evolved additional tolerance to highly variable environments. Intertidal organisms endure alternating marine and aerial exposure and drastic temperature and salinity swings throughout diurnal tidal cycles (Helmuth, 2002; Miller & Dowd, 2019). Multiple adaptations (e.g. behavioural retreat, physiological and phenotypic plasticity) enable diverse communities to thrive where conditions fluctuate (Seebacher et al., 2015; Somero, 2010). Healthy, intact coastal ecosystems, in turn, sustain productive fisheries and unique wildlife populations while regulating fundamental processes (nutrient cycling, carbon sequestration, hydrology) that

maintain environmental balance (Barbier et al., 2011; Choudhary et al., 2024; O'Connor & Crowe, 2005; Trégarot et al., 2024).

2.1.2 Socioeconomic significance

Beyond their ecological value, coastal ecosystems provide enormous benefits to human society. Economically, the 'blue economy' of oceans and coasts has been valued at around US$1.5 trillion per year globally in 2010, reflecting 2.5% of global gross value added, and spanning major industries like fisheries, aquaculture, tourism, shipping, and offshore energy (Organisation for Economic Co-operation and Development, 2016). The same 2016 study projected this contribution to double to roughly US$3 trillion by 2030 (Organisation for Economic Co-operation and Development, 2016). In addition, a 2015 WWF study estimated the gross marine product value to be at least US$2.5 trillion per year globally, based on the ocean's total asset base, consisting of both direct outputs (marine fisheries and coastal ecosystems, marine trade and transport) and more adjacent assets (e.g. tourism and carbon absorption) (Hoegh-Guldberg et al., 2015). This study further emphasises that this is a vast underestimate, due to omission of more intangible yet invaluable features, such as the indirect value of climate regulation, and the role of ocean-based activities such as offshore oil and gas, and wind energy. Coastal resources directly sustain the livelihoods and food security of hundreds of millions of people, and they hold high cultural and recreational importance in many regions (Barbier, 2012, 2017; Barbier et al., 2011).

Human settlement is disproportionately coastal; classic nearshore mapping estimates ~1.2 billion residents within ≤100 km of the shoreline and at ≤100 m elevation, with mean densities roughly three times the global average (Small & Nicholls, 2003). More recent global estimates refine these bands: in 2010–2018, ~38% of people (≈2.86 billion) lived within 100 km of a coast, ≈29% within 50 km, and ≈14–15% within 10 km, with population growth since 2000 strongest closest to the shoreline (Cosby et al., 2024). Moreover, elevation-based exposure metrics likewise report ~625 million people in the ≤10 m low-elevation coastal zone (LECZ) in 2000, and project increases of ~60–70% by 2050 (>1 billion) under Shared Socioeconomic Pathways, with the largest absolute increases in Asia and the highest relative growth in Africa (Merkens et al., 2016; Neumann et al., 2015). Furthermore, recent work finds that coastal infrastructure sits at a median ~392 m from sandy shorelines, with one-third of sandy shorelines having <100 m of infrastructure-free space, and 23–30% of this remaining space projected to be lost by 2100, highlighting ongoing 'coastal squeezing' under

sea-level rise (Lansu et al., 2024). This intense and growing human presence in the coastal zone drives extensive development for housing, infrastructure, and commerce, translating into significant pressures on coastal ecosystems (Airoldi & Beck, 2007; Dafforn et al., 2015). Indeed, many coastal habitats have already been converted or degraded by human use (urbanisation, ports, tourism), with recent estimates suggesting only ~15.5% of the world's coastal regions remain relatively ecologically intact with low human impact (Williams et al., 2022).

2.1.3 Anthropogenic pressures

Coastal ecosystems face numerous pressures that operate and interact across space and time. At the local scale, pollution is a major concern, particularly nutrient-rich runoff from agriculture and untreated (or insufficiently treated) wastewater, which can cause eutrophication in estuaries and coastal waters, alter community assemblages, and fuel algal blooms that deplete oxygen (Lan et al., 2024; O'Connor, 2013; Wurtsbaugh et al., 2019). Diffuse agricultural runoff commonly exports nitrate (NO_3^-) via leaching and tile drains and delivers particulate and dissolved phosphorus through soil erosion and overland flow, whereas municipal/industrial effluents may further discharge ammonium (NH_4^+), dissolved reactive phosphorus, high biochemical oxygen demand, and numerous other co-contaminants (pathogens, pharmaceuticals/antibiotics, microplastics, heavy metals), all of which can intensify eutrophication and degrade coastal ecology in their own right (Carpenter et al., 1998; Edwards et al., 2024; Howarth, 2008; Larsson & Flach, 2021). In 2017, the UN estimated that >80% of total wastewater worldwide was released to the environment without adequate treatment (United Nations World Water Assessment Programme, 2017). By contrast, the UN Sustainable Development Goal (SDG) indicator 6.3.1a (domestic/household wastewater) reported ~56% safely treated in 2024 globally, remaining largely unchanged since 2020, but similarly highlighted persistent treatment gaps once industrial and other non-household sources are included and monitored (UN-Habitat and World Health Organization, 2024). Industrial discharges and oil spills introduce toxic substances, acutely contaminating coastal waters and sediments; for example, heavy oiling of salt marshes after the Deepwater Horizon event in the Gulf of Mexico (2010) increased marsh-edge erosion by ~100–200% for 1–3 years, and greatly impaired vegetation recovery (Silliman et al., 2016; Zengel et al., 2022). Chronic nutrient loading and organic pollution have led to widespread coastal hypoxia and the formation of ecological 'dead zones' in regions of intensive farming and dense coastal populations (Breitburg et al., 2018; Diaz &

Rosenberg, 2008), with knock-on habitat losses such as light-limited seagrass decline (Waycott et al., 2009). Climate change is expected to exacerbate these issues: warming strengthens stratification, reduces O_2 solubility, and increases hypoxia risk in nutrient-enriched systems. As such, coastal hypoxic zones have expanded globally in recent decades as a result of co-occurring climate warming and nutrient runoff (Breitburg et al., 2018; Keeling et al., 2010; Schmidtko et al., 2017).

Biological invasions and overexploitation further compound local pressures. Invasive non-native species can restructure community composition and food webs by outcompeting native species, changing habitat structure, and altering nutrient cycling and sediment stability. For example, in reef systems, invasive lionfish (*Pterois spp.*) exert strong top-down control: in one study, a single fish reduced native reef fish recruitment by ~79% in field experiments, and rapid lionfish population growth coincided with ~65% prey biomass declines in the Bahamas (Albins & Hixon, 2008; Green et al., 2012). Additionally, on high-energy rocky shores across Patagonia, the Northeast Pacific acorn barnacle *Balanus glandula* established in the 1970s and spread rapidly, reshaping traditional intertidal zonation dynamics and displacing native sessile species; it further colonises salt marsh stems at the land–sea interface, and native whelk predators exert little top-down control on it (Pio et al., 2019; Savoya & Schwindt, 2010; Schwindt, 2007). Meanwhile, intense human use of coastal resources (overfishing, shellfish harvesting, excessive tourism) depletes populations and directly disturbs habitats, reducing adaptive capacity and resilience (Lotze et al., 2006; Pauly et al., 1998). Removing key functional groups can restructure trophic interactions; for instance, fishing down food webs and selectively removing herbivores weakens top-down control and fosters macroalgal dominance on reefs (Holbrook et al., 2016; Pauly et al., 1998). At wider habitat scales, harvest methods can damage foundation species: hand-raking and clam digging reduce *Zostera* shoot density and associated carbon storage in seagrass meadows (Barañano et al., 2018; Cabaço et al., 2005) while trawling and dredging disturb benthic communities, seafloor structure, and nutrient cycling processes, especially in fine, low-energy sediments (Bradshaw et al., 2024; Morys et al., 2021). The trampling of salt marshes, mangroves, seagrass beds, and rocky shores, and the extraction of key species (e.g. top predators, herbivores, shellfish) reduce biodiversity and alter trophic interactions, weakening ecosystem resilience (Keough & Quinn, 1998; Rossi et al., 2007; Schlacher & Thompson, 2012; Thompson & Schlacher, 2008). Even non-extractive recreation can be impactful: frequent beach visitation, off-road driving, boating, and close wildlife approaches disrupt

sensitive fauna (e.g. beach-nesting shorebirds and coastal dolphins) via noise, flushing, vessel traffic, and human presence (Larson et al., 2016; Marasinghe et al., 2020; Meyer et al., 2021; Zielinski et al., 2022).

Further key threats to coastal ecosystems include direct habitat modification and loss due to development and land use change (Airoldi & Beck, 2007; Bulleri & Chapman, 2010; Dafforn et al., 2015). Coastal urbanisation often involves constructing infrastructure (seawalls, jetties, ports, roads) and altering landforms (land reclamation, dredging for navigation). These activities disrupt natural sediment dynamics and hydrology, leading to shoreline erosion or sediment accumulation imbalances, and the loss of services that intact habitats provide (Bulleri & Chapman, 2010; Scyphers et al., 2015). For instance, hard armouring (seawalls, bulkheads, dikes) narrows or eliminates intertidal zones and marsh buffers, and simplifies habitat structure (Dafforn et al., 2015). Meta-analysis has further demonstrated that biodiversity and function are typically lower along hardened shorelines relative to natural or nature-based alternatives (Gittman et al., 2016). In parallel, sediment extraction and channel deepening can interrupt alongshore and fluvial sediment supply (van Maren et al., 2015; Žilinskas et al., 2020); global sand and gravel extraction is now on the order of 40–50 billion tonnes per year, with ~4–8 billion tonnes dredged from marine and coastal settings (United Nations Environment Programme, 2019, 2022, 2023; Park, 2024). Studies report coastal impacts including shoreline and delta erosion and sediment-starvation of beaches (Park, 2024; Tamura et al., 2020), nearshore erosion around dredged entrance channels (Žilinskas et al., 2020), and turbidity/sedimentation damage to coral reefs during dredging (Erftemeijer et al., 2012).

Local stressors occur alongside a backdrop of global environmental changes. The ocean is the dominant energy sink in the climate system: it has absorbed over 90% of the excess heat from greenhouse gas forcing, and total ocean heat content set new records successively between 2022 and 2023 (Cheng et al., 2024; Li et al., 2023). Alongside long-term warming, marine heatwaves have increased markedly in frequency and duration, producing ~54% more heatwave days globally between 1925–2016 and driving abrupt biological impacts (Oliver et al., 2018). Furthermore, recurrent bleaching has reorganised coral assemblages at regional scales; extreme warming has collapsed kelp forests and triggered mass seagrass die-offs, with knock-on effects on carbon storage, fisheries production, and coastal food webs (Hughes et al., 2018; Strydom et al., 2020; Wernberg et al., 2016). At the same time, mobile

taxa such as plankton, fishes, and various invertebrates are shifting distributions poleward and to deeper, cooler waters at rates that broadly track local climate velocities, affecting species interactions and ecosystem functioning and creating management challenges as fisheries and conservation targets move across jurisdictional boundaries (Pinsky et al., 2013; Poloczanska et al., 2013). Ocean warming also interacts with oxygen dynamics. Observations show a multi-decadal decline in global ocean oxygen inventories and an expansion of oxygen-minimum zones, while in coastal waters, nutrient enrichment plus stronger stratification worsen the severity and persistence of hypoxic events (Breitburg et al., 2018; Schmidtko et al., 2017). These physical-biogeochemical shifts increase physiological stress, limit habitat for aerobic organisms, and can induce trophic simplification via mass mortality events. Warmer, more stratified, and nutrient-rich seas further elevate risks from harmful algal blooms and infectious diseases; for example, *Vibrio* bacteria are extending their ranges to higher latitudes and longer seasons, with implications for human health and aquaculture (Archer et al., 2023).

Ocean acidification is likewise a pervasive, global-scale pressure on coasts, driven by ongoing uptake of anthropogenic CO_2 and expressed as declining surface-ocean pH and carbonate saturation states. Continued uptake of CO_2 is lowering surface-ocean pH by roughly 0.017–0.027 units per decade, reducing aragonite and calcite saturation states that underpin calcification in corals, coralline algae, molluscs, and many other taxa (Canadell et al., 2021). Long coral core records and global assessments indicate multi-decadal declines in coral calcification and net carbonate production, with projections of widespread transition to net erosional states under higher emission scenarios, even as local contexts and species assemblages modulate outcomes (Cornwall et al., 2021; Davis et al., 2021). These biogeochemical changes compound warming impacts by slowing reef recovery after bleaching and storms and by diminishing the wave-dissipating capacity of reef crests as structural complexity is lost (Ferrario et al., 2014; Harris et al., 2018; Quataert et al., 2015). On rocky shores, comparable sensitivities are reported: intertidal gastropods show impaired embryonic development and disrupted inducible defences at reduced pH (e.g. *Littorina spp.*), and barnacles exhibit slower embryo development and reduced adult survival under elevated CO_2, indicating potential population-level consequences near the range margins (Bibby et al., 2007; Ellis et al., 2009; Findlay et al., 2009, 2010).

Alongside warming and acidification, mean sea-level has already risen by ~0.20 m since 1901, with rates accelerating to ~3.7 mm per year over 2006–2018 (Intergovernmental Panel on

Climate Change (IPCC), 2023), and reaching ~4.77 mm per year over 2014–2023 (World Meteorological Organization, 2024). Under a mid-range pathway, global mean sea-level is projected to be ~0.44–0.76 m higher by 2100, and larger rises are expected under higher emissions scenarios (IPCC, 2023). This upward shift in the baseline converts historically rare extremes into likely more routine events; modelling indicates that by late century, present-day '100 year' water levels will occur at least annually at about half of global tide gauge locations, greatly expanding the reach and damage of flooding events (IPCC, 2023). Greater water depths over reefs, beaches, and wetlands increase wave exposure and inundation stress, altering sediment dynamics and habitat zonation (Trégarot et al., 2024). Coastal wetlands can persist where sediment supply is ample and room exists to migrate landward, but global projections still indicate substantial losses by 2100 where accommodation space is constrained by the aforementioned 'coastal squeezing'; at the same time, warming winters are dictating poleward mangrove expansion at the expense of salt marshes in several regions, reshaping intertidal biogeography and biogeochemistry (Cavanaugh et al., 2014; Saintilan et al., 2014; Schuerch et al., 2018).

2.2 Multiple stressors in space and time

2.2.1 Conceptual overview: defining and classifying multiple stressors

A 'stressor' is generally defined as any external factor or perturbation that causes a quantifiable change in an organism or ecosystem's state beyond its normal range of variability (Crain et al., 2008; Folt et al., 1999). Stressors may be physical (e.g. temperature extremes, habitat disturbance), chemical (pollutant exposure, pH change), or biological (invasive species, disease outbreak) in nature (Darling & Côté, 2008; Folt et al., 1999). Ecosystems and organisms are often exposed to multiple stressors simultaneously or sequentially. When this occurs, the stressors' effects may not simply be independent; their combined impact can interact in complex ways (Crain et al., 2008; Jackson et al., 2021; Orr et al., 2020). Multiple stressor research is concerned with understanding how stressors jointly affect systems, and it classifies interactions by comparing the observed combined effect against an expected baseline derived from each stressor's individual effect (Crain et al., 2008; Folt et al., 1999; Piggott et al., 2015). This baseline is itself a theoretical choice, with ecotoxicological disciplines in particular distinguishing between 'response-addition' (Bliss independence)

versus 'concentration-addition' (Loewe additivity), which embody different assumptions about independence of modes of action of a given dose/stressor. Under Bliss independence, non-interaction assumes stressors act through independent pathways on the same endpoint, so expected joint effects are obtained by combining fractional effects/probabilities. In contrast, under Loewe additivity, non-interaction assumes similar modes of action such that mixtures are dose-equivalent to a higher dose of one stressor (Cedergreen, 2014; Roell et al., 2017; Schäfer & Piggott, 2018).

Under the most common model in ecology, the expected combined effect of two stressors is simply the sum of their separate effects (A + B). Under this model, if the actual joint outcome equals this sum, the combined effect is considered 'additive', i.e. the stressors do not interact in a way that deviates from the null prediction (Folt et al., 1999). Deviations from this null expectation are termed non-additive/non-linear interactions and take two main forms: 1) A 'synergistic' interaction, meaning the combined effect of A + B is *greater* than expected under additivity (i.e. A + B together cause more change than the sum of their individual effects); 2) Conversely, an 'antagonistic' interaction means the combined effect is *less* than expected (one stressor attenuates or partly offsets the effect of the other) (Crain et al., 2008; Darling & Côté, 2008; Folt et al., 1999). These definitions are straightforward when both stressors act in the same direction on a response (e.g. each independently causes a decline in a performance metric, so a 'greater-than-additive' synergism implies a disproportionately large decline, and vice versa for an antagonism). However, if individual stressors have *opposing effects* on a response (for instance, stressor A alone increases growth while stressor B alone decreases it), determining what constitutes 'synergy' versus 'antagonism' becomes more nuanced (Jackson et al., 2016; Piggott et al., 2015; Schäfer & Piggott, 2018). In such cases, the classification can depend on the reference baseline and conventions used, as discussed below. Different researchers have employed different null models (additive vs. multiplicative) and terminologies, which can lead to the same empirical outcomes and ecological mechanisms being labelled differently. Equally, choices of measurement scale/link (identity vs. log/logit) can map 'additive' effects on the link scale to multiplicative effects on the original scale, which can shift the designated control/null, detection thresholds, and potentially alter conclusions (Burgess et al., 2022; Cedergreen, 2014; Dey & Koops, 2021).

Notably, there is no universal standardisation in how multiple stressor interactions are defined and quantified, and the choice of null model, statistical approach, or classification system can influence whether an interaction is detected and how it is categorised. As noted above, most ecological studies have traditionally used the additive null model (simple summation of individual effects) as the baseline, while toxicology often employs an alternative multiplicative model, which accounts for probabilities or percent effects and prevents predicted outcomes from exceeding biological limits (Piggott et al., 2015). The lack of consistency has prompted calls for greater transparency and consistency in multiple stressor research (Jackson et al., 2016; Orr et al., 2020; Piggott et al., 2015). Various studies have developed updated vocabularies and criteria for classifying interactions. For example, Piggott et al. (2015) proposed a directional scheme that resolves cases where classical labels miss nuance, highlighting how differing rulesets can yield different labels for the same biological data and mechanism. Two key illustrative examples warrant focus here: firstly, the term 'negative antagonism', referring to cases where two stressors have opposing single effects, and their combined outcome exceeds the additive null in the direction of the dominant stressor, under which classical definitions would term a synergism; yet here, the combined effect remains less extreme than the independent effect of this dominant stressor itself. Secondly, the authors present the term 'mitigating synergism'; in this case, when both stressors independently act in the same direction, their combined effect flips the response to the opposite direction, and the departure from the additive expectation is greater than the predicted in absolute terms. Piggott et al. argue this is best labelled as a mitigating synergism, as the interaction both reverses the individual effects of both stressors, and exceeds the null in magnitude, i.e. the stressors synergistically inhibit (mitigate) each other's single effects more than would occur under the null model. Further complementing this, Jackson et al. (2016) define a 'reversal' as occurring when the net impact of two stressors is in the opposite direction from that of the sum of their single effects, providing a more general label for sign changes in the combined response relative to the null expectation. Collectively, such refinements in defining stressor interactions highlight that the choice of classification scheme can materially affect reported interaction types and subsequent inferences. To aid interpretation, recent work also recommends direction-aware visualisation (e.g. conditional and marginal plots) and reporting of uncertainty around the null expectation, which helps prevent label ambiguity (Spake et al., 2023). A conceptual overview of classification choices, with numeric examples and directional labels, is provided in Fig. 1.

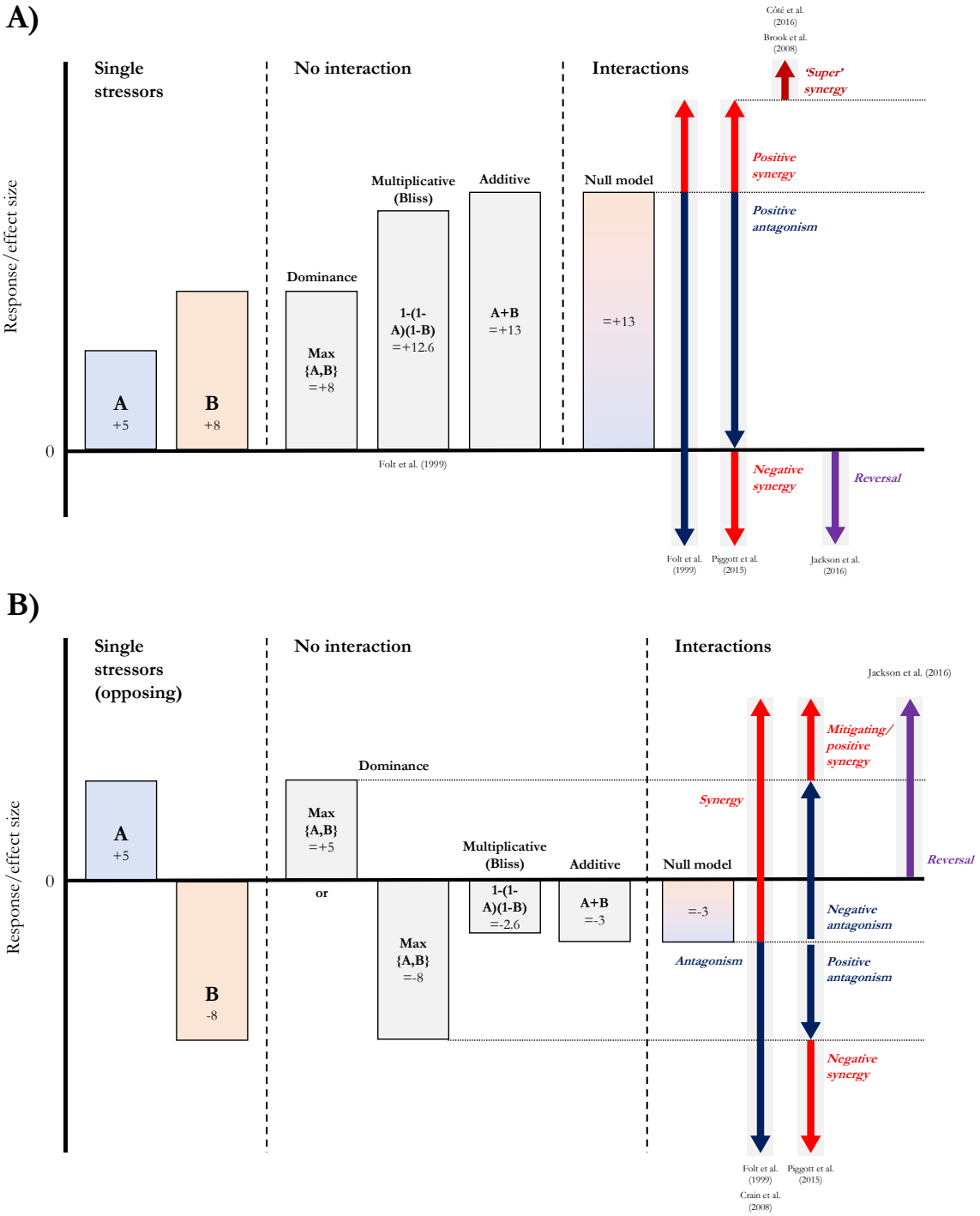

Figure 1 | Summary of key models for defining interactions between two stressors. Bars show single stressor effects in arbitrary units (A, B) and three 'no-interaction' predictions (Folt et al., 1999): comparative/dominance (max{A,B}), multiplicative, and additive null predictions, followed by interaction labels defined relative to the additive null for illustration. Note: some fields use a response-ratio multiplicative convention (combine fold changes as (1 + A)(1 + B) − 1); this figure uses Bliss for independence, consistent with Folt et al. (1999). Further note that a 'multiplicative' null can arise purely from modelling on a log/logit link (effects additive on the link scale but multiplicative when back-transformed), which is a scale choice and not equivalent to the conceptual multiplicative reference model shown here for illustrative purposes. Panel A: both single stressor effects positive (mirrors if both negative). Comparative/dominance = max{A,B}. Multiplicative (Bliss) = 1 − (1 − A)(1 − B), whereby single stressor effects are assumed to be percentages (+5%, +8%) and rescaled to proportions (i.e. A = 0.05, B = 0.08; same logic employed in Panel B). Additive (null) = A + B. Directional labels (Piggott et al., 2015): positive synergism, when the combined effect is more positive than additive; positive antagonism, when it lies between 0 and additive; negative synergism, when the combined effect is negative (opposite in sign to the null; otherwise referred to as a 'reversal' by Jackson et al. (2016)). The dark red arrow marks 'super synergy' (Côté et al., 2016), where the combined effect not only exceeds additivity but also crosses a management/biological threshold (linked to tipping-point framing by Brook et al. (2008)). Panel B: opposing single stressor effects, with a negative additive null. Here, directional labels (Piggott et al., 2015) are anchored to additivity and contextualised by the larger single in the same direction: mitigating/positive synergy when the positive combined effect exceeds the positive single (reversal and enhanced); negative antagonism when the outcome is above the additive null, but not beyond the positive single stressor; positive antagonism when the outcome is below additive but not beyond the negative single stressor; negative synergism, when the negative combined effect exceeds the negative single stressor in magnitude. Reversal denotes a sign flip relative to the additive prediction (Jackson et al., 2016).

Recent efforts have developed tools to help standardise analyses. For instance, Burgess & Murrell (2021) introduced the *multiplestressR* package for R, which automates a rigorous analysis of factorial multiple stressor data. This tool allows users to specify either an additive or multiplicative null model *a priori*, and then classifies interaction outcomes as synergistic, antagonistic, reversal, or null, using a consistent set of formulas and decision criteria. By providing a simple workflow, such tools reduce opportunities for error and make results more comparable across studies. Concurrently, theory and simulations highlight chronic low statistical power for detecting departures from additivity, particularly with small sample sizes and short gradient lengths, and so regardless of the classification system adopted, pre-specifying the null model/scale, and presenting confidence limits around the null margins are highly recommended for transparency and interpretability (Burgess et al., 2021, 2022; Mack et al., 2022; Spake et al., 2023).

Moving beyond static definitions, it is perhaps more useful to focus on understanding the mechanisms that drive interactions, rather than focusing only on classification. Complex interactions can arise from a variety of natural processes: stressors might physically or chemically influence each other (e.g. warmer water holds less dissolved oxygen, worsening hypoxia; or certain pollutants might react to form more toxic compounds in a mixture) (Breitburg et al., 2018; Diaz & Rosenberg, 2008). Likewise, biological mechanisms such as physiological trade-offs within organisms, species interactions, or longer-term adaptation and acclimation can all cause the net effect of multiple stressors to deviate from additivity (Crain et al., 2008; Darling & Côté, 2008). On the other hand, some apparent interactions can stem from how we measure or model effects rather than any true ecological synergy. For example, using an inappropriate null model or failing to account for nonlinear stress-response relationships can create the illusion of an interaction where none exists biologically (Piggott et al., 2015; Schäfer & Piggott, 2018). Distinguishing such artefacts from genuine ecological interactions is essential. Advancing multiple stressor ecology requires not only consistent definitions and rigorous statistical approaches, but also a push toward mechanistic, process-based understanding (Todgham & Stillman, 2013). This will improve our ability to predict and interpret combined effects in new contexts, and to better inform management on the nature and mechanisms of interactions. For instance, knowing that two stressors strongly synergise to damage a habitat would underscore the importance of addressing both together, whereas if one stressor's impact is largely antagonised by another, management could focus on the dominant stressor first (Crain et al., 2008; Jackson et al., 2016). Thus, clarity in concepts and

consistency in methodology are foundational for tackling the complex reality of multiple stressors.

2.2.2 Context dependence and complexity

The interaction between a given pair of stressors can vary greatly depending on the context. Here, context spans organismal/ecosystem biotic traits and histories (e.g. thermal tolerance, life stage, trophic position) together with baseline abiotic conditions (e.g. background temperature or nutrient levels, natural disturbance regimes), which collectively can shift the null expectation, alter the likelihood of apparent non-additivity, and change both the direction and magnitude of any deviations (Jackson et al., 2016; Orr et al., 2020; Spake et al., 2023; Walther, 2010). For example, earlier life stages often display heightened sensitivity to combined stressors relative to adults, and trophic position can modulate how effects propagate through interaction networks (Beauchesne et al., 2021; Byrne & Przeslawski, 2013; Kroeker et al., 2013). This context dependence typically weakens when assessed at higher levels of biological organisation and broader spatial scales with greater ecological complexity (Hoppit & Schmidt, 2022; Walther, 2010). Greater biodiversity, for instance, can buffer aggregate responses via biological insurance and asynchrony, helping explain why community-level metrics may appear more antagonistic or buffered than individual organismal responses under the same stressors (Loreau & de Mazancourt, 2013; Schnabel et al., 2021; Yachi & Loreau, 1999). In general, as ecological complexity increases, there are more pathways for indirect effects and compensatory responses that can dampen or counteract the direct physiological impacts of stressors (Côté et al., 2016; Walther, 2010). Feedbacks, species interactions, and biodiversity-driven compensation can redirect or buffer organism-level responses, so the emergent pattern can differ compared to what a simpler organismal extrapolation would suggest (King et al., 2022; Loreau & de Mazancourt, 2013). Meta-analyses indeed find that population-level metrics (e.g. abundance or vital rates) tend to show more synergistic responses, whereas community-level metrics (e.g. diversity, total biomass) more often show antagonistic or buffering responses (Crain et al., 2008; Jackson et al., 2016; King et al., 2022; Maher et al., 2019; Orr et al., 2020).

Because most experimental studies necessarily limit the number of factors they manipulate, it is critical to consider how ambient environmental modifiers might influence findings (Stewart et al., 2013; Todgham & Stillman, 2013). In a controlled two-stressor (2×2) experiment, the outcome may hinge on the specific conditions under which it was conducted.

For example, background climatic and ecological differences between or within regions across timescales could lead to different interaction outcomes for the same pair of stressors (Walther, 2010). Thus, two-factor experiments may be interpreted against a broader environmental backdrop, treating natural context variables not as abstract 'context', but as potential moderators of stressor effects (Jackson et al., 2016; King et al., 2022). For instance, on rocky shores, steep gradients in microclimate occur over small spatial scales (due to tidal height, sun exposure, wave action, habitat heterogeneity), and these gradients can influence both baseline stress and organisms' subsequent sensitivity to additional stressors (Bauer et al., 2024; Choi et al., 2019; B. Helmuth et al., 2016; Kunze et al., 2021). Methodologically, this argues for designs that treat moderators explicitly (e.g. factorials crossed with gradient/regression designs, hierarchical models that include site-level covariates) and for greater visualisation of null margins across main effects and covariates to better contextualise outcomes (King et al., 2022; Spake et al., 2023). Incorporating such natural variability into experimental designs or comparative analyses can greatly improve generality. In practice, this might mean replicating experiments across multiple locations or conditions, or explicitly including a range of background values for key factors (e.g. conducting experiments during both cool and warm seasons, or at sites with low vs. high nutrient background levels). Crucially, when >2 context variables (including additional stressors) co-vary, higher-order interactions and dimensionality effects become common, further reducing the transferability of simple pairwise inferences (Bi et al., 2024; Diamant et al., 2023; Rillig et al., 2019). Incorporating environmental context echoes calls in the literature to place multiple stressor ecology within a larger spatial and ecological framework for better inference and upscaling of results (Kefford et al., 2023; Stockbridge et al., 2025).

Another aspect of context is the exposure regime of stressors: whether stressors occur as chronic pressures or short pulses, and whether they occur simultaneously or sequentially (Brooks & Crowe, 2019; Stewart et al., 2013; Todgham & Stillman, 2013; Vos et al., 2023). Timing can alter both the magnitude and, in some cases, the direction of multiple stressor interactions. For example, in eutrophication-impacted estuaries, a heatwave that coincides with, or follows, periods of low dissolved oxygen can have disproportionately strong effects relative to the same warming event under well-oxygenated conditions, because higher temperatures increase metabolic O_2 demand and raise organisms' oxygen thresholds (i.e. reduce hypoxia tolerance). As a result, changing the overlap, order, or lag between warming and pollution-driven deoxygenation can push communities onto different trajectories,

further shaped by subsequent community- and ecosystem-level feedbacks (Breitburg et al., 2018; Vaquer-Sunyer & Duarte, 2008). Likewise, a moderate stressor that occurs repeatedly (chronic exposure) might allow some acclimation, whereas the same stressor as an acute pulse might overwhelm organisms and interact more strongly with other stressors present at that moment (Rodgers et al., 2025; Todgham & Stillman, 2013). Empirically, both the order and the delay between stressors have been shown to shift interaction type, and analytical approaches that model exposure duration and non-linearity can recover these regime-dependent effects (Brooks & Crowe, 2019; King et al., 2022). Moreover, because physiological rates scale with temperature and resources, metabolic constraints can also generate predictable context dependence in time and across baselines (Jackson et al., 2021).

At larger spatiotemporal scales, context can further include a system's resilience (distance to a tipping point) and whether positive feedbacks create alternative stable states; in such systems, the same pair of stressors can tip a system over a given threshold at one place and time, but not another, because slower variables (e.g. legacy nutrients, grazer biomass, connectivity) can shift the threshold and produce hysteresis (Carpenter et al., 2011; Carpenter & Brock, 2006; Scheffer et al., 2001, 2009). For instance, nutrient enrichment and warming may flip an aquatic system to a turbid state only where legacy contaminants are present, whereas similar loads elsewhere may remain clear (thresholds detected with early-warning indicators in whole-ecosystem tests) (Carpenter et al., 2011; Sondergaard et al., 2001; Taranu et al., 2018). Likewise, on coral reefs, overfishing, pollution, and heatwaves may collectively trigger macroalgal regimes primarily where herbivory is depleted, but not where it is intact (Adam et al., 2015; Hughes et al., 2007). Moreover, in estuaries, the mouth state (intermittently open vs. closed) sets flushing/residence time and stratification, thereby modulating how nutrient loading and warming co-produce deoxygenation and concentrate pollutants, so identical stressor forcing can yield different interaction types (Cronin-O'Reilly et al., 2024; McSweeney et al., 2017; Shen et al., 2022; Testa et al., 2022).

In addition to context dependence, methodological issues can hinder capturing the complexity of interactions. Underpowered experimental designs and truncated stressor gradients are common issues that can reduce the ability to detect interaction effects (Burgess et al., 2022). One analysis suggests that typical sample sizes in many studies are inadequate to detect anything but the strongest synergistic or antagonistic effects (Burgess et al., 2022). Moreover, as noted earlier, inconsistency in null model choice can lead to misclassification

of interactions (Jackson et al., 2016; Piggott et al., 2015). To improve inference, recommendations suggest fully crossed, multi-level factorial designs where logistically feasible and ecologically valid, sufficient replication to achieve statistical power, and explicit tests of how sensitive conclusions are to statistical choices (Burgess et al., 2022; Piggott et al., 2015). Complementary strategies include pre-specifying moderators and null assumptions, using hierarchical meta-analytic models that include context terms, and diagnosing robustness to exposure-regime choices (Brooks & Crowe, 2019; Spake et al., 2023). By addressing these design considerations, studies will be more comparable and results more robust. Bridging the gap between controlled experiments and real-world complexity is necessary if multiple stressor science is to support effective, informed management decisions.

2.2.3 Marine and coastal multiple stressor research

A landmark meta-analysis by Crain et al. (2008) synthesised 171 marine and coastal multiple stressor experiments, reporting that roughly one-third of the cases showed synergistic effects (36%), one-third antagonistic (38%), and the remainder additive (26%), with an overall slightly synergistic trend across all studies. Patterns varied systematically with response level and trophic group; population-level endpoints tended to be more synergistic, community-level endpoints were often antagonistic or additive, and heterotrophs were more often synergistic than autotrophs. Notably, adding a third stressor altered outcomes in roughly two-thirds of comparisons and roughly doubled the proportion of synergies (from ≈33% to ≈66%), underscoring how interaction structure can change as complexity increases. However, the frequency and classification of interaction types has been challenged by more recent work. Most notably, Piggott et al. (2015) applied a direction-aware classification system (as outlined in §2.2.1) to the 2008 Crain et al. dataset, and standardised the calculations used to assign interaction classes. Specifically, they: rejected Crain's rule for 'opposing-effect' cases (in which calculations only counted synergy when the combined effect was more *negative* than the additive expectation); recomputed interaction contrasts under a consistent additive effects model that tracks both the magnitude and direction of the cumulative response; and introduced and then identified examples of 'mitigating synergism' (where the combined response reverses the sign of single-stressor effects, and also departs more from the additive expectation than predicted). When this direction-aware and standardised framework was applied to the same dataset, the balance of classes shifted; fewer synergies (≈31% vs. 36%) and more antagonisms (≈43% vs. 38%), demonstrating how interaction frequencies depend on both the rule set and the way opposing-effect cases are computed and labelled.

Nevertheless, both studies highlight that non-additive outcomes are pervasive in marine systems, therefore, treating stressors independently risks bias in both inference and management (Crain et al., 2008; Darling & Côté, 2008; Krishna et al., 2025; Stockbridge et al., 2020; Villar-Argaiz et al., 2018).

Following Crain et al.'s 2008 study, the volume of multiple stressor experiments in marine ecology has expanded sharply (Gissi et al., 2021; Halpern et al., 2015). However, the modal study remains a laboratory or mesocosm trial on a single species or narrow community under highly controlled settings (Gissi et al., 2021; Halpern et al., 2015; Krishna et al., 2025; Todgham & Stillman, 2013). Scope biases are pronounced and evident in recent meta-analyses: Gissi et al. (2021) found that studies are unevenly distributed geographically, with over two-thirds occurring in the Northern Hemisphere (67.6%), concentrated in the Temperate Northern Atlantic (46.1%) and Northern Pacific (14.7%), with entire realms such as the Tropical Eastern Pacific lacking regional analyses; spatially, more than half are sub-national in extent (52.3%), with only 6.5% spanning multiple biogeographic realms. Evidence is also taxonomically and thematically skewed toward readily tractable organisms and a narrow set of stressor pairs: recent work by Krishna et al. (2025) found that phytoplankton and bivalves are the most frequently studied groups, and temperature is the most common focal stressor at the species level; small-bodied taxa are disproportionately tested in controlled labs (>50%), whereas seagrass studies are predominantly *in situ* (<20% lab). These distributions mirror content biases: climate-related stressors, especially warming, are over-represented (often paired with other climate stressors such as acidification), while key coastal stressors such as eutrophication and associated hypoxia are comparatively understudied (Gissi et al., 2021; Krishna et al., 2025). Mechanistically, the prominence of warming is expected due to how pervasive it is: higher temperatures raise ectotherm metabolic demand while reducing oxygen solubility and, via stronger stratification, limit oxygen resupply, representing physical-physiological couplings that make warming a potent co-factor with other stressors (Duncan et al., 2023; Rubalcaba et al., 2020; Vajedsamiei et al., 2021).

Syntheses reiterate that adding a climate stressor often amplifies local anthropogenic stressors, particularly at organism and population scales, while also noting substantial context dependence in response metrics (Gissi et al., 2021; Krishna et al., 2025). A recent synthesis by Krishna et al. (2025) underscores these patterns: warming, acidification, eutrophication, and metal pollution recur as critical pairwise combinations (with phytoplankton especially

sensitive to warming × metals × nutrients, and bivalves to warming × low pH) and further calls for broader community- and ecosystem-level work that couples field realism with mechanistic platforms. Mechanisms align with these outcomes: when warming co-occurs with hypoxia, organisms already near oxygen thresholds can face elevated metabolic costs; in nutrient-rich, stratified waters, heatwaves may intensify deoxygenation and harmful algal blooms; and in calciferous organisms such as bivalves, warming plus low pH impairs acid-base regulation and shell growth. Such patterns are reflected in observed coastal deoxygenation trends in systems like Chesapeake Bay, the Baltic Sea, and the Gulf of Mexico (Breitburg et al., 2018; Diaz & Rosenberg, 2008; Gissi et al., 2021; Krishna et al., 2025; Vaquer-Sunyer & Duarte, 2008). Together, these lines of evidence caution against overgeneralisation: warming often acts as a force multiplier, but its efficacy at any given place and time hinges on the system-specific context, and the level of biological organisation measured.

A consistent theme in the multiple stressor literature is divergence of outcomes across ecosystem scale. At the species level, responses reflect direct effects on physiology, life history, and distributions, but community outcomes are also shaped by indirect, interaction-mediated effects (e.g. shifts in predation, competition, facilitation). Empirical work shows that biotic interactions can redirect multiple stressor outcomes: in a benthic community, species interactions altered the net response to concurrent warming and acidification (Legrand et al., 2017), and in kelp systems, warming interacting with an invasive species redirected trophic links in ways that favoured kelp persistence via positive feedbacks (Miranda et al., 2019). At broader food web scales, modelling and mesocosm work indicates climate warming can weaken energy transfer to higher trophic levels and simplify webs, amplifying risks under multiple stressors (Ullah et al., 2018; Yin et al., 2024). While meta-analyses document taxon-specific sensitivities across benthos and drivers (Hoppit & Schmidt, 2022), these wider patterns are consistent with the IPCC Sixth Assessment Report (AR6) of multi-trophic impacts and context dependence in coastal systems (IPCC, 2023). Furthermore, mobility modulates exposure and community/ecosystem dynamics at the coast: sessile and low-mobility taxa often bear greater acute thermal and chemical loads than motile consumers that can seek refuge, altering how stress signals propagate through food webs (Hayford et al., 2021; Virgin & Schiel, 2023). Collectively, bridging studies that explicitly couple direct physiology with interaction-driven pathways are essential for robust upscaling across scales of impact.

Manipulative multiple stressor studies must balance experimental control with ecological realism. Laboratory and *ex situ* mesocosm platforms enable fully crossed designs, strong replication, and mechanistic attribution (e.g. bioenergetic limits, thresholds), making them indispensable for testing interaction null models and physiological pathways (Stewart et al., 2013; Todgham & Stillman, 2013). However, their major drawback is ecological realism: enclosure artefacts, simplified communities, and damped variance in covarying drivers can limit transferability to nature (Sasaki et al., 2025; Stewart et al., 2013; Todgham & Stillman, 2013). A major advance has been variability-aware mesocosms that replay realistic diurnal/seasonal fluctuations and covarying temperature × pH × O_2 × light, shrinking the gap and revealing responses that static models may miss (Gerhard et al., 2023; Pansch & Hiebenthal, 2019). New combined mesocosm model efforts also recover day-night carbonate variability and interaction effects under warming × acidification, further shrinking lab–field gaps (Ullah et al., 2024). For intertidal ecology specifically, the recently developed Intertidal Environmental Chamber (IEC) offers a bench-based, open-source system that realistically reproduces coastal tidal cycles and emersion/immersion thermal trajectories, light intensities, and water exchange, useful for mechanistic multiple stressor tests in the context of highly variable environments (Pereira et al., 2025). These advances narrow lab–field gaps, but realism, cost, and scalability constraints still limit broad *ex situ* generality (Sasaki et al., 2025). Comparatively, *in situ* experiments embed manipulations in natural communities and microhabitats, capturing ambient variability and biotic interactions that can strongly mediate multiple stressor outcomes. On rocky shores, passive intertidal warming via substrate colour (dark vs. light) has been shown to reliably raise peak emersion surface temperatures by ~2–3 °C, shifting settlement, competition and trophic mediation; such work has shown, for example, that herbivory can buffer warming-driven community change (Kordas et al., 2015; Kordas & Harley, 2016; Lathlean & Minchinton, 2012). A complementary route could leverage ambient stressor gradients (e.g. distance from sewage outfalls, river plumes) to study nutrient enrichment and co-occurring contaminants under real hydrodynamics. Methodological trade-offs remain: for instance, passive warming is inexpensive and scalable, but yields weather-dependent, asymmetric warming and microclimate side effects; other methods face feasibility constraints of installation and maintenance, replication, disturbance (e.g. trampling or removal studies) and control of co-varying drivers (Sasaki et al., 2025).

2.2.4 Rocky shores as model experimental systems

Rocky intertidal shores are globally distributed, accessible 'natural laboratories' where steep, repeatable physical gradients (tidal height, emersion time, wave exposure) make mechanisms tractable and manipulations feasible (Helmuth et al., 2016). Historically, rocky shores helped found modern experimental ecology: Connell's barnacle transplants established how competition and physical stress set zonation; Paine's *Pisaster* sea star removals introduced the keystone predator concept; Dayton's space-limitation and disturbance experiments formalised the role of physical events; and Lubchenco's tidepool herbivory work showed how consumer preferences modulate algal diversity (Connell, 1961; Dayton, 1971; Lubchenco, 1978; Paine, 1966). Collectively, these examples helped inspire the Menge–Sutherland environmental-stress model that links top-down, bottom-up and stress gradients (Menge & Sutherland, 1976, 1987). This classic work still frames rocky shore research on stress-interaction coupling and regime shifts, with modern long-term programmes now linking it to climate change: for instance, the 'MarClim' project is the most spatio-temporally extensive time series of rocky intertidal ecosystems globally, documenting poleward shifts and community reconfigurations across shores (Mieszkowska et al., 2021). Contemporary extremes in warming further underscore this relevance: for instance, the June 2021 Pacific Northwest heatwave produced record anomalies and widespread intertidal mortality, illustrating how thermal events intersect with classic interaction webs (White et al., 2023).

Biophysically, intertidal organisms occupy dual media (water and air), so body temperatures often decouple from ambient air or water and instead track solar loading, tide timing, morphology and aspect (Helmuth et al., 2016; Seabra et al., 2011). Moreover, microhabitat topography and aspect generate °C-scale thermal mosaics that can exceed regional means, shaping community distribution and the realised local exposure to multiple stressors. Recent syntheses map this fine-scale thermal stress and its consequences for community assembly (Seabra et al., 2011; Wang et al., 2020). Early mechanistic work showed how to predict these operative body temperatures from heat-budget physics (short- and long-wave radiation, convection, conduction, evaporation) and tide phase, with peak exposures frequently occurring around midday low tides rather than at meteorological maxima (Helmuth, 1998, 2002). Building on these models, biomimetic 'robomussel' loggers have been field-deployed since the late 1990s, and were formalised by Fitzhenry et al. (2004) as epoxy shells with embedded thermistors matched to organism size/shape and thermal inertia. These biomimetic loggers provide inexpensive, long-duration *in situ* proxies that typically track live

animals within ~1–2 °C, and now underpin a global dataset spanning 1998–present (Helmuth et al., 2016). Alongside more recent developments of complementary 'robolimpets' and 'robobarnacles', pairing these records with organism-centred heat-budget models allows researchers to quantify exceedance of sublethal/lethal thresholds and to ground-truth predictions at biologically relevant scales (Chan et al., 2016; Helmuth et al., 2016; Lima & Wethey, 2009).

Crucially, rocky shore interaction networks including competition for space, grazing control, predator-prey dynamics, facilitation, and trait-mediated effects, modulate how stressors propagate through communities, making these systems even more appropriate for diverse multiple stressor insights across scales and contexts (Gribben et al., 2019; Jurgens et al., 2022). Classic and contemporary experiments show that grazers (e.g. patellid limpets, littorinids) strongly regulate early algal stages and canopy development: removing grazers releases opportunistic and fucoid algae, reorganising low-shore assemblages and altering competitive outcomes (Caronni et al., 2019; Kordas et al., 2017). Wave exposure and recruitment regimes shift the balance between fucoid algae, barnacles, and grazers, yielding different stable states across shores (Chemello et al., 2018; Dudgeon & Petraitis, 2022; McCabe & Konar, 2021). Predator effects go beyond density alone: trait-mediated interactions, e.g. crab or fish cues that suppress snail feeding, cascade to algal cover and composition, changing the sign or magnitude of net effects at higher orders of ecosystem organisation (Gravem & Morgan, 2016). Top-down × bottom-up coupling is also pervasive: factorial field tests and syntheses show that nutrient enrichment and consumer pressure interact to set macroalgal diversity, biomass and even ecosystem functions, with the direction and strength of control shifting with productivity, exposure and depth (Gagnon et al., 2016; Korpinen et al., 2007; Spiecker & Menge, 2024). Foundation species amplify these dynamics: mussel beds and canopy-forming seaweeds engineer microclimates, buffer heat/desiccation, trap sediments and create habitat for rich invertebrate assemblages: facilitation can strengthen under heatwaves and generate facilitation 'cascades' that transmit positive effects across trophic levels (Gribben et al., 2019; Jurgens et al., 2022; Montie & Thomsen, 2023; Westerbom & Koivisto, 2022). These interaction webs directly condition multiple stressor responses. For instance, herbivory can buffer community reorganisation under experimental warming, preserving competitive structure and dampening warming impacts (Kordas et al., 2017). The experimental legacy of rocky shores, together with their strong and repeatable environmental gradients and observability, makes them uniquely tractable systems for

multiple stressor experiments, which are scalable, replicable, and mechanistically interpretable across physiology to community dynamics (Denny et al., 2011; Hawkins et al., 2020; B. Helmuth et al., 2016; Kunze et al., 2021).

2.3 Integrating multiple stressors into coastal management

2.3.1 Underrepresentation in current frameworks

Scientific understanding of multiple stressors has advanced rapidly, yet policy and management frameworks have lagged in translating this knowledge into practice (Hodgson et al., 2019; Hodgson & Halpern, 2019; IOC-UNESCO, 2022). Traditional environmental management remains largely siloed by sector or issue, with disjointed policies for water quality, fisheries, coastal development, and climate change, despite clear evidence noted above that coastal ecosystems experience combined pressures rather than isolated threats (Côté et al., 2016; Crain et al., 2008; Gissi et al., 2021; Halpern et al., 2008, 2015; Krishna et al., 2024). At the highest levels, most governance frameworks still treat stressors in isolation, or when multiple stressors are considered, the scope is often incomplete. For example, a 2022 UNESCO-IOC policy brief provided a broad overview of multiple ocean stressors and endorsed ecosystem-based management (EBM) as an ideal approach, but its recommendations remained general with limited specificity for the land–sea coupled challenges of coastal zones, in favour of more abstract open-ocean concepts (IOC-UNESCO, 2022). Likewise, major international agreements such as the United Nations Convention on the Law of the Sea (UNCLOS), the Paris Agreement, the UN Framework Convention on Climate Change (UNFCCC), and the Convention on Biological Diversity (CBD, and associated Aichi Targets and Kunming–Montreal Global Biodiversity Framework) set overarching environmental targets (e.g. emissions reduction, area-based conservation), yet contain no explicit operational requirements to evaluate cumulative or interactive impacts on coastal ecosystems (Convention on Biological Diversity, 2010, 2022, 2024; 2022; United Nations, 1982, 1992, 2015). In practice, this leaves many jurisdictions without a legal obligation to address non-linear multiple stressor effects, reinforcing a focus on single activities managed in isolation (Hodgson et al., 2019). UNCLOS, for instance, mandates that states consider potentially harmful environmental impacts (Art. 206) but does not explicitly require or acknowledge cumulative effects assessment or embed an ecosystem

approach (United Nations, 1982). Notably, only very recently has a new international instrument, the 2023 High Seas Treaty (United Nations, 2023), sought to explicitly consider cumulative impacts within environmental impact assessments (EIAs) in areas beyond national jurisdictions (ABNJ), a gap that highlights how current frameworks have until now failed to mandate integrated approaches (High Seas Alliance, 2023).

This compartmentalised approach is reinforced by institutional silos. Frequently, different agencies or laws govern land-based sources of stress (e.g. riverine pollution, coastal land use) versus offshore marine resources, resulting in fragmented management that can overlook cross-sector synergies and compounding impacts (Appleby et al., 2024; Bremer & Glavovic, 2013; Kelly et al., 2019; Singh et al., 2021; Yuan & Chang, 2021). A prime example is New Zealand: coastal and marine management there is spread across more than 25 statutes implemented by at least 14 agencies and authorities, each with narrow mandates. The result is a fragmented regime that complicates any comprehensive, multiple stressor management (Brake & Peart, 2015; Bremer & Glavovic, 2013; Hewitt et al., 2022). Similarly, in British Columbia (Canada), efforts to tackle marine pollution must coordinate among numerous bodies (federal fisheries, federal shipping, provincial environment, agriculture, local land use planners), with demonstrable misalignment between these agencies meaning one agency's actions can inadvertently undermine another's goals (Singh et al., 2021). The result of such institutional fragmentation is often inconsistency and blind spots in management: local stressors (e.g. runoff, habitat loss) and global stressors (e.g. climate change) might be addressed separately, missing their combined or interactive effects. As aforementioned, multiple stressors can interact in complex, non-additive ways, which single-issue, uncoordinated management structures risk ignoring. Yet, most governance frameworks remain piecemeal, hampered by inconsistent legislation, overlapping jurisdictions, and silo thinking, all cited as key barriers to effective cross-sector, cumulative-effects management (Aiken et al., 2025; Appleby et al., 2024; Kelly et al., 2019; Wurtsbaugh et al., 2019).

From a management perspective, several implications emerge. Ignoring non-additive interactions can risk estimations that understate cumulative impacts where synergies occur, and overstate them in the case of antagonism or dominant stressor scenarios, potentially misallocating resources and efforts (Côté et al., 2016; Crain et al., 2008; Jackson et al., 2016; Stockbridge et al., 2025). One practical solution is to pair cumulative effects assessments with explicit prioritisation that targets such driving stressors, rather than spreading resources

uniformly (Stockbridge et al., 2025). In parallel, because local, tangible stressors (such as pollution, overfishing, habitat disturbance) are often those with the capacity for immediate action, reducing them is generally a 'no-regrets' strategy in the face of global change (IPCC, 2023). For instance, improving water quality and habitat condition can increase the resilience of coral reefs to withstand marine heatwaves (Harley et al., 2006; Trégarot et al., 2024; Voolstra et al., 2023). Mitigating a local stressor can substantially buffer the impact of a climate stressor if the two act synergistically, essentially buying time or capacity for adaptation (Jackson et al., 2016). Notably, however, if the interaction is antagonistic, local mitigation may have less benefit (or potential costs), or might only be effective in areas that are climate refugia (Brown et al., 2013; Côté et al., 2016). This logic is driving many climate adaptation plans to include local conservation actions as a cornerstone tool, with the IPCC AR6 endorsing this "local levels for resilience" approach (IPCC, 2023). Lastly, methodological choices in how evidence is gathered matter for its usefulness. A combination of aforementioned mechanistic lab studies and field validation yields the best insights for management outputs (Binning et al., 2025; B. Helmuth et al., 2016; Pansch & Hiebenthal, 2019; Todgham & Stillman, 2013). By integrating both, research can better forecast real-world outcomes and provide management with information on not just direct effects, but also the likelihood of indirect cascade effects or context contingencies.

2.3.2 Integrated management approaches

In recent years, there has been growing recognition that coastal management must move toward integrated, ecosystem-based strategies to deal with multiple stressors. EBM is often highlighted as a guiding paradigm: by definition, it is an integrated approach that considers the entire ecosystem, including humans, and inherently accounts for cumulative impacts, trade-offs, and cross-scale linkages (Long et al., 2015; Sander, 2023). Many national and regional policies and conventions now endorse EBM in principle as a best practice for managing multiple ocean uses and stressors (Haugen et al., 2024; Papadopoulou et al., 2025). For coastal zones specifically, EBM principles manifest through frameworks like Integrated Coastal Zone Management (ICZM) and cross-sector marine planning initiatives. ICZM aims to coordinate actions across the land–sea interface, recognising that activities upstream (in watersheds) directly affect coastal water quality and habitats, and vice versa. By integrating management across terrestrial and marine jurisdictions, ICZM seeks to overcome the institutional fragmentation that plagues coastal governance (Bremer & Glavovic, 2013; Jiang et al., 2023; Kelly et al., 2019; Yuan & Chang, 2021). However, even these 'integrated'

approaches can fall short if implemented within unchanged bureaucratic structures. Enduring issues like sectoral silos, competing objectives, power imbalances, and policy layering can dilute their effectiveness; the underlying governance system must also evolve to truly scale up effective multiple stressor management (Kelly et al., 2019; Tafon, 2018).

Marine Spatial Planning (MSP) has emerged as a practical tool to operationalise multiple stressor management in space and time. MSP is a process of allocating marine and coastal areas for specific uses (conservation, fishing, shipping lanes, energy infrastructure) based on explicit consideration of ecological values and human pressures. A core goal of MSP is to reduce conflicts and cumulative impacts by separating incompatible activities and limiting the intensity of use in sensitive areas, thereby proactively managing the combined footprint of human activities (Ehler & Douvere, 2009; Ehler, 2021; Frazão Santos et al., 2024, 2025). In Europe, the regulatory architecture actively promotes such integrated approaches: the Water Framework Directive (WFD, 2000/60/EC) requires integrated river-basin management to achieve 'good ecological status' in inland and coastal waters, meaning countries must identify and address all significant pressures in each watershed in a unified plan (European Commission, 2000). The Marine Strategy Framework Directive (MSFD, 2008/56/EC) extends this to marine waters, explicitly mandating that member states assess the predominant pressures and impacts on their seas, including an analysis of "the cumulative and synergistic effects" of human activities, as a partial basis for attaining 'good environmental status' (European Commission, 2008; Puharinen, 2023). In parallel, the EU's Maritime Spatial Planning Directive (2014/89/EU) obliges countries to develop marine spatial plans that apply an ecosystem-based approach, balancing blue economy growth with environmental sustainability (European Union, 2014). These instruments together have driven the adoption of cumulative impact mapping and cross-sector 'programmes of measures' in many European coastal regions (European Environment Agency, 2019). Early evidence indicates that such integrated efforts are yielding results: for example, nutrient pollution inputs and fishing pressure have declined in some European seas over the past decade, partly attributable to WFD/MSFD measures addressing co-occurring stressors jointly (European Environment Agency, 2019). That said, implementation remains uneven. New MSP and ICZM initiatives are often constrained by persistent problems, including competing sectoral priorities, inconsistent metrics of success, and limited integration with parallel terrestrial planning (Botero et al., 2025; Mcateer et al., 2022). In practice, fully integrating land and sea management is challenging, and even progressive policies can fall

short of true integration if not backed by strong coordination mechanisms and political will (Kelly et al., 2019; Tafon, 2018).

Within the toolkit of integrated management, marine protected areas (MPAs) and related area-based measures play a key role in addressing multiple stressors at local scales. MPAs are designated zones where certain harmful activities (e.g. fishing, dredging, mining) are restricted or banned to conserve biodiversity and ecosystem function. By definition, MPAs can explicitly include intertidal as well as subtidal areas: the widely adopted IUCN definition covers "any area of the intertidal or subtidal terrain, together with its overlying water and associated [...]" (Kelleher, 1999). In practice, this intertidal coverage is operationalised in national implementations: for instance, in the UK, Marine Conservation Zones (MCZs) list intertidal habitats among their protected features (e.g. 'intertidal mudflats' in the Erme Estuary MCZ) (DEFRA, 2019); and in New Zealand, marine reserves are defined in law as 'specified areas of the sea and foreshore', i.e. extending onto the intertidal (Marine Reserves Act, 1971). By design, MPAs directly alleviate local stressors such as overfishing, habitat destruction, and pollution, with the goal of enhancing natural resilience and economic sustainability in the face of global stressors like climate change (Davis et al., 2019; Frazão Santos et al., 2025; Humphreys & Herbert, 2018; Lester et al., 2009; Selig & Bruno, 2010). The effectiveness of MPAs, however, depends strongly on their design and management. A global analysis of 87 MPAs by Edgar et al. (2014) found that conservation outcomes increased markedly when reserves had five key features: no-take status, strong enforcement, age greater than 10 years, large size (>100 km^2), and isolation from fished areas by natural barriers. Reserves meeting at least four of these five criteria had dramatically higher biomass of fish and top predators: on average, 5× more large fish and 14× more sharks, compared to similar areas open to fishing, whereas most MPAs lacking these features were ecologically indistinguishable from unprotected sites. These findings underline that to maximise stress reduction, MPAs must be sufficiently stringent, long-term, and well-managed (Edgar et al., 2014). When local stressors are minimised, ecosystems maintain more of their structure and function, which in turn can buffer against external shocks. For example, coral reef reserves with abundant herbivorous fish are far less likely to shift to algal-dominated states after a climate-driven bleaching event than neighbouring overfished reefs (Mumby et al., 2007; Selig & Bruno, 2010). Likewise, protected coastal wetlands such as mangrove forests and salt marshes continue to accrete sediment and mitigate storm surges as seas rise, whereas

degraded wetlands may lose elevation or collapse, exacerbating flood risks (Kirwan & Megonigal, 2013; Narayan et al., 2016).

There is mounting evidence that well-managed marine reserves also enhance ecosystem resilience to global stressors. A comprehensive review by Roberts et al. (2017) concluded that MPAs can help marine ecosystems and coastal communities adapt to at least five prominent climate change impacts, (namely ocean acidification, sea-level rise, intensifying storms, shifts in species distributions, and deoxygenation) by safeguarding carbon-rich habitats, reducing non-climate stresses, and providing refugia that foster genetic and ecological resilience and connectivity (Roberts et al., 2017). Empirical case studies support this: for instance, a fully protected reserve at Isla Natividad (Baja California, Mexico) showed higher resistance and faster recovery of shellfish populations following a climate-driven hypoxia mass mortality event, compared to adjacent fished areas. The reserve's large, protected abalone broodstock produced sufficient offspring to quickly repopulate the site, buffering the community against collapse and yielding spillover effects to the surrounding region (Micheli et al., 2012; Roberts et al., 2017). While protected areas are not a 'solution' for global problems, they can locally mitigate multiple human impacts, thereby giving marine ecosystems capacity to cope with external stresses. This recognition underpins calls by scientists and policymakers to greatly expand effective MPA coverage (e.g. the '30×30' target of protecting 30% of the ocean by 2030) as part of a climate-ready, cumulative effects management strategy (Convention on Biological Diversity, 2022).

In forward-looking coastal plans, multiple levels of integration can be combined to address multiple human impacts (see Tables 1 and 2 for a summary of key management approaches and tools applicable to coastal zones). EBM can serve as the broad paradigm defining the overall goals (e.g. maintaining ecosystem health and services while allowing sustainable use) and articulating system-wide trade-offs. ICZM can ensure explicit coordination between watershed authorities, coastal zone managers, and offshore regulators, aligning land-based and marine policies so that, for example, agricultural nutrient management and coastal water quality targets are jointly designed to combat eutrophication and biodiversity loss. MSP then provides a spatial blueprint to distribute human uses in a way that prevents 'hotspots' of cumulative pressure. Finally, targeted measures are implemented to address specific stressors: these include well-managed MPAs, sustainable fisheries quotas, water quality regulations, habitat restoration projects, and other potentially nature-based solutions. Notably, many

coastal regions are now investing in nature-based solutions and tools like living shorelines and habitat restoration because of their multi-benefit nature (Dario et al., 2024; Paxton et al., 2024). Replanting mangroves or salt marshes and rebuilding oyster reefs, for instance, can simultaneously reduce erosion and flooding (often providing better long-term shoreline protection than hard seawalls), filter out nutrients and pollutants from runoff, provide nursery habitat that boosts fisheries, and sequester carbon in sediment, thereby addressing physical, chemical, and ecological stressors in tandem (Daro Justine & Seenath, 2025; Onorevole et al., 2018; Perricone et al., 2023).

However, fully operationalising multiple stressor management remains challenging and often requires overcoming significant institutional inertia. It demands sustained monitoring with iterative adjustment, cross-agency cooperation, and adequate resources to implement integrative approaches. In practice, progress is incremental, but the elements are coming together. For example, the High Level Panel for a Sustainable Ocean Economy called for all exclusive economic zones (EEZs) to be managed under sustainable, ecosystem-based plans by 2025 (High Level Panel for a Sustainable Ocean Economy, 2023). As of the most recent updates, nine of the Ocean Panel's 18 member countries are implementing or updating Sustainable Ocean Plans, and additional plans from remaining countries were expected by the end of 2025 (e.g. Jamaica, Kenya, Norway, Portugal) (High Level Panel for a Sustainable Ocean Economy, 2024); the Panel has also launched a '100% Alliance' inviting all coastal states to deliver Sustainable Ocean Plans by 2030, signalling that while the 2025 members' milestone catalysed progress, completion both within and external to the Panel remained uneven (High Level Panel for a Sustainable Ocean Economy, 2025). Achieving this vision requires aligning traditionally separate sectors and mandates, linking agricultural policy with coastal conservation plans, and embedding climate adaptation measures into local land use decisions. It also means establishing feedback loops where management actions are regularly evaluated and adjusted in light of new scientific information or observed outcomes, keeping the strategy adaptive as conditions change (High Level Panel for a Sustainable Ocean Economy, 2023, 2025). While much progress remains, these integrated frameworks and tools show a clear intent to move beyond fragmented, single-issue management toward a more coordinated approach that can better handle interactive impacts facing coastal ecosystems.

2.3.3 Bridging the science–policy interface

Translating the complex science of multiple stressors into effective policy is an ongoing challenge. One key issue is science–policy communication: decision-makers need access to clear, actionable information on how stressors interact, where cumulative impacts are greatest, and which interventions will yield the best outcomes, delivered in a way that fits management and legislative timelines (European Environment Agency, 2020; Hodgson et al., 2019). In response, scientists are developing various tools and frameworks, including network-based models that map out stressor-response pathways, risk assessment methods for cumulative effects, and scenario-testing decision-support systems for spatial planning, to bridge research and decision-making (Ehler and Douvere, 2009; Ehler, 2021; European Environment Agency, 2020; Wedding et al., 2022). A 2012 study from coastal Mexico provides an empirical example of reserve design enhancing post-disturbance recovery, illustrating how strategic interventions can target leverage points in multiple stressor contexts (Micheli et al., 2012). Ensuring such scientific insights reach and inform decision-makers is crucial. Encouragingly, some jurisdictions are beginning to require cumulative effects assessments (CEAs) as part of environmental planning and project approvals (European Commission, 2008; Impact Assessment Act, 2019). In practice, however, practitioners often report that while ecological aspects of cumulative effects are sometimes considered, social and economic dimensions are neglected, in part due to fragmented data and unclear responsibilities across agencies. To bridge this gap, research has called for developing unified assessment frameworks that explicitly integrate ecological and human factors, and for establishing common indicators and threshold levels that can serve as early warnings and trigger management action before irreversible harm occurs (European Environment Agency, 2020; Kelly et al., 2019; Wedding et al., 2022).

Given the uncertainty and dynamic nature of multiple stressor impacts at the land–sea interface, management must also be flexible and learning-oriented. This means adopting an adaptive management approach: regularly monitoring key indicators of ecosystem health (e.g. water quality, oxygen levels, habitat extent, keystone species populations), evaluating the system's responses to both management actions and external drivers, and adjusting strategies as new information emerges or conditions change (Birgé et al., 2016; Smit et al., 2021). It also means anticipating that certain combinations of stressors may produce unexpected or sudden effects, and preparing contingency measures in advance. Such contingency measures require solid scientific understanding (linking multiple stressors to ecological thresholds) and

proactive planning, so that managers have the legal and logistical ability to act quickly when warning signs appear (Wedding et al., 2022). Developing early-warning indicators for detrimental stressor interactions is an active area of research; for example, indicators of approaching ecological tipping points have been proposed and tested in aquatic systems (Carrier-Belleau et al., 2023; Dakos et al., 2024). Another crucial point is that climate change must be embedded within local planning and not treated as a separate issue, because climate-driven factors often amplify other stressors. Coastal managers therefore need strategies that both mitigate local stressors and facilitate resilience to global changes. This dual approach is increasingly endorsed in coastal governance circles. Similarly, guidance for 'climate-proofing' coastal infrastructure and restoration projects emphasises solutions that reduce local vulnerabilities (like wetland restoration for flood protection) while accounting for future sea-level rise and other climate shifts (Bongarts Lebbe et al., 2021; Steven et al., 2020). By integrating climate adaptation directly into multiple stressor management rather than addressing climate in isolation, coastal plans can ensure that efforts to reduce local stressors are not undermined by evolving baseline conditions.

Effective multiple stressor management also demands inclusive, cross-sector stakeholder engagement. Because the drivers of coastal degradation span many sectors (fisheries, agriculture, urban development, industry, transportation), solutions must involve a broad coalition of actors, from government agencies at all levels (national, regional, local) to local communities and Indigenous groups, scientists, non-governmental organisations, and industry stakeholders (de Oliveira et al., 2024; Hernández-Delgado, 2024; Lukambagire et al., 2024). Inclusive planning processes, as particularly noted in EBM and MSP frameworks, help ensure that diverse knowledge systems (including local and traditional knowledge) are considered, and that management actions are socially acceptable and economically feasible. Early and genuine stakeholder involvement can also pre-empt conflicts by uncovering potential trade-offs and points of friction before decisions are finalised. Reviews and comparative studies consistently identify insufficient stakeholder engagement and weak governance support as impediments to effective implementation; conversely, where users perceive legitimacy and share in the benefits, compliance and outcomes improve markedly (Bennett, 2016; Davis et al., 2017; Gutiérrez et al., 2011; Kelly et al., 2019). Bridging the science–policy gap therefore requires deconstructing institutional silos and improving coordination across agencies and sectors, aligning mandates (e.g. ensuring that water, agriculture, and fisheries departments share overlapping objectives for coastal health), and

empowering local managers and communities with informed knowledge and the authority to act on multiple stressors in a direct, adaptive way (Kelly et al., 2019; Singh et al., 2021).

The current trajectory of coastal management is moving from a fragmented, single-issue approach toward integrated, adaptive approaches that account for cumulative effects. There is clear momentum in both scientific and policy communities for this paradigm shift, as evidenced by emerging frameworks (EBM, ICZM, MSP), new legislative requirements (e.g. the MSFD's mandate to consider cumulative impacts), and the proliferation of tools like cumulative impact mapping and climate-inclusive planning. Yet significant work remains to turn these high-level concepts into consistent on-the-ground practice. Success will depend on continued improvements in scientific understanding (for example, clarifying interaction mechanisms and identifying critical thresholds or tipping points), the development of user-friendly decision-support tools, and the political will and institutional capacity to implement holistic management despite short-term pressures and inertia. By actively linking multiple stressor science to management actions, investing in adaptive capacity, and treating coastal ecosystems as interconnected social–ecological systems, policymakers can begin to close the gap between what research shows is needed and what management delivers.

Management Approach	Description	Key characteristics	Key challenges	Illustrative examples
Ecosystem-Based Management (EBM)	An approach that considers whole ecosystems, including people, to maintain ecosystem health and services. It addresses cumulative stressors and promotes sustainable practices through adaptive management and stakeholder involvement.	• **Holistic view:** Manages physical, biological, and human components as a whole. • **Adaptive management:** Flexible, iterative; adjusts to new data and conditions. • **Stakeholder involvement:** Engages communities, industry, and governments for collaborative decisions and shared responsibility. • **Sustainability focus:** Balances ecological health with economic and social goals for long-term sustainability.	• **Integration into existing frameworks:** Requires significant changes to established policies. • **Balancing time horizons:** Preventing short-term gains from compromising long-term ecosystem health. • **Data and monitoring:** Needs extensive, ongoing data to inform adaptive management. • **Interdisciplinary coordination:** Complex coordination across sectors with differing methods, objectives, and terms.	National Marine Sanctuaries (USA). Coral Triangle Initiative (Southeast Asia).
Marine Spatial Planning (MSP)	An approach to strategically allocate the spatial and temporal distribution of human activities in marine areas, aiming to reduce conflicts, improve coordination, and ensure sustainable resource management.	• **Spatial and temporal allocation:** Allocates activities to minimise conflicts and optimise space. • **Ecosystem-based management:** A tool to implement EBM. • **Adaptive management:** Flexible, iterative; adjusts to new data, conditions, and uses. • **Stakeholder involvement:** Engages fisheries, tourism, conservation, and shipping for informed decisions. • **Sustainability focus:** Balances ecological, economic, and social goals for long-term sustainability. • **Multi-level governance:** Aligns policies across jurisdictions for consistency and coherence.	• **Data availability:** Needs reliable spatiotemporal data; gaps reduce planning accuracy. • **Interdisciplinary coordination:** Complex cross-sector work with differing methods, objectives, and terms. • **Legal and policy alignment:** Harmonising with existing frameworks is complex and time-consuming. • **Implementation costs:** Resource-intensive to develop and implement.	European Union MSP Directive. Great Barrier Reef Marine Park zoning framework (Australia; hybrid MPA/MSP example).
Integrated Coastal Zone Management (ICZM)	A coordinated approach to sustainable coastal management that integrates policies and practices across sectors such as tourism, fisheries, and urban development, aiming to balance environmental, economic, and social objectives.	• **Holistic land–sea approach:** Integrates terrestrial and marine environments across the coastal interface. • **Stakeholder involvement:** Engages fisheries, tourism, conservation, and shipping for informed decisions. • **Adaptive management:** Flexible, iterative; adjusts to new data and conditions. • **Sustainability focus:** Balances ecological, economic, and social goals for long-term sustainability. • **Land–sea stakeholders:** Includes fisheries, tourism, land use, and shipping along the interface.	• **Implementation complexity:** Multidisciplinary scope makes coordination and integration difficult. • **Interdisciplinary coordination:** Differing methods, objectives, and terms hinder coordination. • **Data and information gaps:** Comprehensive coastal data often lacking due to limited funding and outdated monitoring. • **Policy and legal frameworks:** Effectiveness depends on supportive laws, which vary by region and create inconsistencies.	Netherlands National Spatial Strategy and Third Policy Document on Coastal Areas. Mediterranean ICZM Protocol.
Marine Protected Areas (MPAs)	Designated marine areas established to protect and conserve biodiversity, ecosystems, and cultural values. These areas are managed through regulations that limit human activities to protect marine life and habitats.	• **Conservation focus:** Conserves biodiversity, protects ecosystems, and maintains cultural heritage. • **Legal protection:** Laws restrict activities such as fishing, mining, and tourism. • **Specific boundaries:** Defined areas with protections. • **Biodiversity preservation:** Protects species, habitats, and ecosystems from harm. • **Ecosystem services:** Maintains cultural heritage and key ecosystem services.	• **Enforcement and compliance:** Limited resources, remoteness, and weak monitoring hinder adherence. • **Balancing conservation and livelihoods:** Protect ecosystems while considering local economies and rights. • **Interdisciplinary coordination:** Complex cross-sector coordination with differing methods, objectives, and terms.	Papahānaumokuākea Marine National Monument (USA). Ross Sea Marine Protected Area (Antarctica).

Table 1 | Heuristic overview of key coastal management approaches. This summary is illustrative rather than exhaustive; examples include implemented approaches, policy instruments, and hybrid frameworks where relevant.

Management tool	Description	Key characteristics	Key challenges
Seawalls and breakwaters	Structures that protect coastlines from wave action and erosion. Help maintain coastal infrastructure by reducing erosion and flooding, preserving land use and habitats.	• **Provide immediate and long-lasting protection:** Typically concrete or rock, creating a robust barrier for infrastructure and settlements. • **Effective in high-energy environments**: Suitable for areas with strong waves or heavy storms.	• **Can increase downstream erosion:** Reflect wave energy, causing scouring in adjacent areas. • **Installation and maintenance:** High upfront costs, logistical effort, and ongoing upkeep. • **Disrupt sediment transport:** Can alter beach dynamics and adjacent ecosystems.
Living shorelines	Use natural materials (vegetation, sand, rock) to stabilise shorelines. Promote habitat creation and heterogeneity, improve water quality, and offer adaptive, sustainable erosion control.	• **Natural materials:** Use native vegetation, sand, and rocks to stabilise shorelines in a sustainable, adaptive way. • **Habitat creation:** Provide heterogeneous habitats across the land–sea interface. • **Improved water quality:** Filter pollutants and sediments from runoff. • **Climate resilience:** Flexible structures that evolve with change, boosting resilience to sea-level rise and storms.	• **High initial costs and maintenance:** Significant investment with continuing upkeep. • **Regulatory complexity:** Permitting can be difficult to navigate. • **Public perception and ecological uncertainty:** Resistance from limited awareness; uncertainty about long-term ecological outcomes and invasive species.
Artificial reefs	Submerged structures that mimic natural reefs. Enhance habitats and biodiversity, supporting fisheries and recreation.	• **Habitat enhancement:** Provide shelter and breeding grounds, supporting biodiversity and fisheries. • **Biodiversity support:** Attract diverse marine life and create complex ecosystems. • **Recreational and economic benefits:** Enable diving and fishing, boosting local economies and awareness.	• **High initial costs and maintenance:** Significant investment and ongoing upkeep. • **Site selection and environmental impact:** Must avoid habitat disruption, toxins, or navigation hazards. • **Regulatory and permitting issues:** Complex, often involving multiple agencies.
Dune restoration	Rebuild and stabilise sand dunes with vegetation and other materials. Provide natural buffers to storm surges, supporting resilience and biodiversity.	• **Natural buffer to storm surges:** Dunes absorb and dissipate wave energy, limiting flooding and erosion. • **Stabilisation with vegetation:** Native plants bind sand and reduce erosion. • **Support for biodiversity:** Create habitats for plants and animals, aiding ecosystem health.	• **High initial costs and maintenance:** Significant investment with continuing upkeep. • **Regulatory complexity:** Permitting can be challenging. • **Human impact and access:** Managing foot traffic and development is difficult. • **Site-specific design:** Requires careful, site-tailored planning to avoid impacts and ensure success.
Mangrove reforestation	Plant and restore mangrove forests to protect coasts from erosion and storm surges. Enhance carbon sequestration, provide habitat, and support fisheries.	• **Coastal protection:** Natural barriers against erosion and storm surges. • **Carbon sequestration:** Highly effective at capturing and storing CO_2. • **Habitat and fisheries support:** Critical habitats that sustain biodiversity, fisheries, and livelihoods.	• **Site selection:** Needs suitable salinity, tidal flow, and soils. • **Invasive species and pests:** Vulnerable to biotic threats; requires monitoring. • **High initial costs and maintenance:** Significant investment and ongoing care. • **Regulatory complexity:** Permitting can be difficult.
Silt curtains	Barriers that control sediment spread during coastal construction. Protect habitats from sedimentation, supporting sustainable development and water quality.	• **Sediment control:** Limit sediment plumes during works, protecting water quality and habitats. • **Habitat protection:** Safeguard reefs, seagrasses, and other sensitive ecosystems. • **Support sustainable development:** Enable projects while mitigating impacts.	• **Installation and maintenance:** Proper setup and upkeep needed in currents, tides, and weather. • **Site-specific design:** Custom designs for local conditions complicate planning. • **High initial costs and maintenance:** Significant investment and ongoing care. • **Effectiveness in high-energy areas:** Strong currents or waves reduce performance. • **Regulatory complexity:** Permitting can be challenging.
Beach nourishment	Add sand or sediment to combat erosion and maintain beach width. Enhances protection and recreational value, supporting tourism and shoreline management.	• **Erosion control:** Replenishes eroding beaches, countering shoreline loss. • **Coastal protection:** Strengthens natural barriers against surges and high tides. • **Recreational and aesthetic value:** Maintains beach width and quality, supporting tourism and local economies.	• **High costs and funding:** Sourcing, transport, and placement are expensive; replenishment recurs. • **Environmental impact:** May disturb habitats or introduce mismatched materials. • **Sustainability and longevity:** Storms and tides can quickly remove added sand. • **Regulatory complexity:** Permitting can be time consuming. • **Sediment source and quality:** Must match existing beach to minimise impacts.

Oyster reef restoration	Create or restore oyster reefs to improve protection, water quality, and biodiversity. Reefs act as natural breakwaters and enhance habitat and local income streams.	• **Coastal protection:** Reefs reduce wave energy and erosion, limiting surge impacts. • **Water quality improvement:** Oysters filter pollutants and excess nutrients. • **Biodiversity and habitat:** Complex structures that support diverse marine species and resilience.	• **High initial costs and maintenance:** Significant investment and ongoing care. • **Site selection and suitability:** Needs appropriate salinity, depth, and substrate. • **Regulatory complexity:** Permitting can be difficult. • **Vulnerability to pollution and disease:** Sensitive to water quality, diseases, and invasives; requires monitoring.
Seagrass bed replanting	Restore or plant seagrass to stabilise sediments, enhance water quality, and support marine life. Seagrass provides critical habitat and sequesters carbon.	• **Sediment stabilisation:** Roots and rhizomes hold sediments and maintain seabed integrity. • **Water quality enhancement:** Filter nutrients and suspended pollutants. • **Habitat and biodiversity:** Critical habitats that support coastal species and ecosystem function. • **Carbon sequestration:** Capture and store CO_2, aiding climate mitigation.	• **High initial costs and maintenance:** Significant investment and ongoing care. • **Site selection and suitability:** Requires suitable depth, salinity, and light. • **Regulatory complexity:** Permitting can be challenging. • **Vulnerability to stressors:** Sensitive to water quality, temperature, and disturbance.
Marine debris removal	Programmes and tools to remove litter and debris from coasts and seas. Reduce pollution, protect wildlife, and engage communities in conservation.	• **Pollution reduction:** Remove debris, lowering ecosystem harm. • **Wildlife protection:** Reduce entanglement, ingestion, and habitat disruption. • **Community engagement:** Mobilise local clean ups, building awareness and responsibility.	• **Resource-intensive:** Requires funding, manpower, and specialised equipment. • **Logistical difficulties:** Accessing remote sites and ensuring proper disposal or recycling. • **Continuous effort:** Ongoing issue needing sustained commitment. • **Regulatory complexity:** Permitting can hinder larger-scale removals

Table 2 | Heuristic overview of selected coastal management tools and interventions. This summary is illustrative rather than exhaustive and includes a broad range of intervention types used to reduce pressures, manage risk, or support ecological recovery in coastal systems.

2.4 Thesis aims and objectives

The literature review highlights three linked gaps. First, the marine multiple stressor evidence base is still dominated by controlled lab and mesocosm studies that simplify real-world variability, even though interaction strength and sign often hinge on timing and realistic environmental fluctuations; moreover, choices and reporting of analytical methods (null model, scale, classification) remain inconsistent. Second, generality is unresolved: responses are strongly context dependent across time, space, and levels of biological organisation, yet coordinated, community-level *in situ* experiments replicated across biogeographic realms are rare. Third, policy instruments recognise cumulative effects in principle, but operational treatment of interactions across the land–sea interface is uneven, constrained by sectoral silos and fragmented mandates; practical guidance for embedding interactive effects logic in spatial planning is still lacking.

The overarching aim of this thesis was to investigate the impacts of multiple stressors on coastal ecosystems, using approaches across the science–policy interface. Specifically, I

employed a scalable, cost-effective *in situ* experimental method at a rocky shore to study temporal variability in independent and interactive impacts of warming and nutrient pollution at the local scale across multiple levels of ecosystem organisation (Chapter 3), further synthesised with biogeographic context dependencies in the direct and indirect mechanistic responses of community groups across 11 global locations, with 22 total sites (Chapter 4). Insights from these results and the wider literature were then used to integrate multiple stressor science within locally actionable management strategies to ensure greater harmonisation and efficacy of marine spatial planning at the coastal zone (Chapter 5).

2.4.1 Chapter summaries

- **<u>Chapter 3:</u> Gene-to-Population Level Responses to Multiple Stressors on the Rocky Shore**

Coastal eutrophication and warming frequently co-occur on temperate rocky shores, yet community-level, experimental field evidence of multiple stressor impacts is comparatively scarce. This chapter uses a factorial, *in situ* design to test how simulated warming and local nutrient enrichment independently and interactively influence the composition of key intertidal groups (barnacles, grazing gastropods, macroalgae, microphytobenthos groups (including green microalgae, cyanobacteria, and diatoms)), as well as trophic pathways and genetic responses across multiple levels of ecosystem organisation. Key objectives are to: 1) quantify independent and interactive effects on functional-group responses and cover across a summer growing season, and uncover temporal trends across and within the season; 2) evaluate whether nutrient enrichment modulates thermal sensitivity; and 3) use barnacles as a case study to further trace potential bottom-up/top-down pathways using trophic (stable isotope analyses) and genetic indicators (gene transcriptomic analyses).

- **<u>Chapter 4:</u> Global Intertidal Community Responses to Warming and Nutrient Enrichment**

In this chapter, I investigate whether, and to what extent, spatial biogeographic context mediates the magnitude and direction of stressor interactions. To test this generality vs. context dependence, I scale the *in situ* passive warming methodology from Chapter 3 globally via a coordinated network of 22 rocky shore field sites. Objectives are to: 1) assess whether categorical warming and nutrient enrichment

produce consistent community responses (barnacles, grazing gastropods, macroalgae) across regions, or whether outcomes are heterogeneous and context dependent by site, and to what magnitude/direction; 2) quantify how local environmental conditions (local weather covariates, surrounding land use, broader biogeographic groupings) and the magnitude of realised local stressor treatments modulate site-specific responses; and 3) explore direct and indirect biotically mediated stressor pathways among functional community groups (barnacles, grazers, macroalgae). Taken together, Chapters 3 and 4 link within-season local temporal dynamics to spatial, biogeographic context dependence across multiple ecosystem groups and levels of organisation.

- **<u>Chapter 5:</u> Balancing the Blue Economy and Multiple Stressor Management in Marine Spatial Planning at the Land–Sea Interface**

Governance frameworks increasingly promote MSP and EBM but often lack explicit, operational treatment of interactive effects, especially across the land–sea boundary where terrestrial activities drive marine exposures. Motivated by the temporospatial evidence from Chapters 3 and 4, this chapter draws on the wider policy and planning literature to examine how MSP can better incorporate multiple stressor management within the wider context of the emergent blue economy, focusing on enabling conditions, decision processes, and practical tools that embed interactive-stressor thinking, climate adaptation and nature-based solutions across space and time. Objectives are to: 1) review international and national policy architectures for provisions on cumulative/interactive effects and land–sea integration; 2) identify key components (e.g. impact assessment within MSP, cross-agency coordination, indicators, participatory processes) that increase the feasibility of MSP to address multiple interacting stressors across space and time; and 3) practically apply these components to a case study (Massachusetts, USA) to illustrate how current planning instruments and sectoral policies can be operationalised within our identified components to reduce overlapping stressors, whilst advancing sustainable blue economy goals.

2.4.2 Integrated thesis: status of manuscript submissions

This thesis follows the integrated route, comprising the provided introduction and literature review, three research chapters constructed as academic papers submitted for publication in peer-reviewed journals, and a collective discussion and conclusion chapter. Each respective paper has been reformatted for inclusion within the thesis with a consistent typeface and citation/referencing style, but each remains faithful to its respective manuscript submission regarding journal mandates on word count and structure. Each chapter is preceded by commentary text to contextualise and integrate the paper into the thesis, so that the entire thesis can be read as a single, coherent document. Furthermore, each research chapter contains a respective statement of authorship, which also includes data availability statements where appropriate to access supplementary data frames and code as required. The status of each manuscript submission is detailed below.

Chapter 3: Gene-to-Population Level Responses to Multiple Stressors on the Rocky Shore

- **Status:** Published in *Ecology and Evolution* (doi.org/10.1002/ece3.73368).

Chapter 4: Global Intertidal Community Responses to Warming and Nutrient Enrichment

- **Status:** In review at *Communications Biology*.

Chapter 5: Balancing the Blue Economy and Multiple Stressor Management in Marine Spatial Planning at the Land–Sea Interface

- **Status:** Published in *npj Ocean Sustainability* (doi.org/10.1038/s44183-026-00192-3).

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3

Research Article

Chapter 3 | Gene-to-Population Level Responses to Multiple Stressors on the Rocky Shore

3.0 Commentary and statement of authorship

Chapter 3 provides the thesis' first experimental evidence of how coastal ecosystems respond to multiple stressors, treating the nature of stressor interactions as potentially time-varying and expressed differently across levels of biological organisation. In doing so, this chapter establishes novel insights that link organism-level indicators to community outcomes within a single manipulative field design. The rocky intertidal is used here because it remains one of the most empirically tractable coastal systems, while also being strongly structured by exposure regimes, hydrodynamics, thermal variability, and pulsed resource inputs that can cause stressor effects to shift over both short and seasonal timescales (Harley et al., 2006;

Hawkins et al., 2020, 2023; Hesketh & Harley, 2023). The chapter therefore foregrounds temporal dynamics and multi-level inference as core features of the multiple stressor design.

The study is situated within a UK governance context in which sewage pollution and coastal water quality remain high-profile and actively contested policy concerns. National reporting indicates that only a minority of estuaries, and fewer than half of coastal waters, achieve 'good ecological status', consistent with persistent enrichment pressures alongside other drivers (Environment Agency and Natural England, 2025). Storm overflow discharges also remain a recurrent management issue, reinforcing that short-duration contamination pulses can operate as a chronic pressure at the national scale (Burnett & Bolton, 2025). Within this setting, the Peacehaven (East Sussex) system provides a relevant land–sea interface context for evaluating a locally expressed enrichment pressure against a climatic warming backdrop.

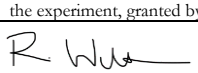
Methodologically, Chapter 3 adapts a low-cost passive warming approach developed for intertidal settlement plates, using black versus white high-density polyethylene surfaces to generate consistent field-based warming contrasts while remaining compatible with dense replication and repeated surveys (Kordas et al., 2015; Kordas & Harley, 2016). A fully factorial multiple stressor experiment was implemented by deploying this warming manipulation across adjacent shore locations that differ in sewage-associated nutrient levels, yielding a warming × enrichment contrast that can be tracked through the summer survey period. Furthermore, alongside the main manuscript (§3.0–3.5) and supplementary information (§3.6), a supplementary how-to-build document (§3.7; reformatted for inclusion in this thesis) provides standardised construction details to support reproducibility and transferability of the methodology, as later employed in Chapter 4.

As the opening research chapter, the Peacehaven experiment establishes two thesis-wide links. First, it provides a scalable experimental template and an explicit analytical vocabulary for interpreting stressor interactions through time and across ecological levels. Second, it motivates the shift from describing stressor effects to explaining context dependence by demonstrating that interaction signals can vary across responses, organisational levels, and seasonal stages. These links are then expanded in Chapter 4, which retains the core field method while shifting inference from within-site temporal dynamics to cross-site heterogeneity at a global biogeographic scale, and to the biotic and abiotic mechanisms through which stressor effects propagate through communities.

Statement of Authorship

Title of Paper	Gene-to-Population Level Responses to Multiple Stressors on the Rocky Shore
Publication Status	✓ Published □ Accepted for Publication □ Submitted for Publication □ Unpublished and unsubmitted work written in a manuscript style
Publication Details	Manuscript details Title: Gene-to-Population Level Responses to Multiple Stressors on the Rocky Shore. Status: Published in *Ecology and Evolution* (doi.org/10.1002/ece3.73368). • The submitted version within this thesis includes both the material of the published manuscript, alongside additional revisions following doctoral viva examination. Author list Ramesh Wilson, Katie Driver, James Orr, Manuela Truebano, Michael Collins, & Michelle C. Jackson. Data accessibility statement The ecological datasets and analysis code supporting this paper, including RNA-seq annotated differential-expression and GO enrichment output workbooks, are archived at Zenodo (https://doi.org/10.5281/zenodo.18121767) and maintained in the associated GitHub repository. Raw transcriptome sequencing data are available via ArrayExpress (Accession: E-MTAB-16541). Public sewage release records are available via Southern Water's Rivers and Seas Watch portal (Newhaven outfall; https://experience.arcgis.com/experience/e9a1db8d193d4cd582d550285a3aeb44/page/Map/). Precipitation time series used for SI Fig. S10 were downloaded from Visual Crossing and are not redistributed in the public repository as per third-party terms; users can obtain equivalent raw data directly from Visual Crossing (https://www.visualcrossing.com/weather-query-builder/). Ethics statement No animal ethics approval was sought as this study did not involve vertebrates, and it did not involve regulated 'protected animals' under common legal frameworks governing animal research. In the UK, the Animals (Scientific Procedures) Act 1986 applies to living vertebrates and living cephalopods as protected animals, while EU Directive 2010/63/EU similarly applies to live non-human vertebrates and live cephalopods. The focal taxa in this study (barnacles, non-cephalopod gastropods, macroalgae and microphytobenthos) fall outside those scopes. The study also did not involve captivity, invasive procedures, or deliberate harm beyond exposure to natural field conditions and passive settlement-plate manipulation. Permission for field installation was granted by Natural England and the Crown Estate.

Student confirmation

Student Name	Ramesh Wilson (RW)		
Contribution to the Paper	RW co-developed the project concept (with MCJ) and designed, organised, constructed, and implemented the field experiment. RW led fieldwork logistics and undertook all field sampling and ecological measurements, with additional field sampling support from KD, JO and MCJ. RW led the analysis, modelling, interpretation, and synthesis of all ecological and stable isotope datasets, produced all figures, and compiled the Supporting Information. RNA-seq processing and bioinformatic/transcriptomic analyses were led by MT and MC; Novogene provided transcript assembly, and MC compiled the transcriptomic supplementary outputs. RW led the ecological interpretation of the transcriptomic results and integrated these findings with the ecological and stable isotope outcomes. RW wrote the full draft of the manuscript and led revisions, submission, and correspondence. Acknowledged non-author support: P. Ditchfield provided technical support for stable isotope sample processing; Novogene provided transcript assembly; P. Sanders, D. Edwards, and A. Jackson supported installation. We are grateful for permission to install the experiment, granted by Natural England and the Crown Estate.		
Signature		**Date**	11/01/2026

Supervisor confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor Name and Title	Dr. Michelle Jackson (Associate Professor of Freshwater/Marine Ecology)		
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3.1 Abstract

Coastal ecosystems are exposed to both global and local stressors operating across multiple scales. However, research rarely considers how their combined effects propagate over time and across levels of biological organisation. Here, we employ an *in situ* warming experiment across two rocky shore sites with contrasting sewage pollution to quantify independent and interactive effects of warming and nutrient pollution from genes to populations. Passively warmed and control settlement plates were deployed at polluted and non-polluted sites and surveyed across a summer to quantify temporal dynamics in the responses of key intertidal taxa. Barnacles were further employed as a model for comparing responses across biological levels, including body size, stable isotope analysis, and RNA sequencing. Pollution consistently increased invertebrate abundance and macroalgal cover, alongside transient positive effects on barnacle size, whereas warming reduced barnacle abundance and suppressed macroalgal cover late in the season. Warming and pollution interacted synergistically on barnacle abundance, with pollution remaining the dominant stressor. Microphytobenthos groups similarly showed distinct pollution-driven increases with warming primarily modifying temporal trajectories; cyanobacteria showed both date-specific and season-wide synergistic interactions against a backdrop of temporal variability across stressor treatments. Consistent with these patterns, pollution shifted barnacle $\delta^{13}C$ and $\delta^{15}N$ towards values indicative of greater assimilation of sewage-derived material, while warming increased elemental C:N ratios, consistent with altered nutritional stress. Barnacle transcriptomic responses mirrored this dominance of pollution, broadly regulating gene expression linked to protein turnover, DNA repair and protein folding; combined warming and pollution further intensified proteostasis-related changes and produced predominantly reversal and antagonistic interaction types. Our results show that sewage pollution can overwhelm and reshape warming effects over time and across biological levels, linking group-level responses with parallel shifts in trophic biomarkers and gene regulation. Our scalable field approach provides a template for *in situ* marine multiple stressor experiments across wider spatiotemporal scales.

3.2 Introduction

Anthropogenic stressors are rapidly degrading natural ecosystems. These stressors include both global drivers, such as climate change-related processes including warming and ocean acidification, and local pressures, such as nutrient pollution, tourism, and land use. As a result, multiple stressor research has rapidly emerged as a key area of concern in global change biology (Orr et al., 2020), aiming to understand the combined and potentially interactive effects of co-occurring stressors on ecosystem structure and function. Combined stressor effects may be additive or may deviate from additivity through synergistic or antagonistic interactions, whereby the net response is greater or smaller than expected from the independent effects of each stressor alone. Such non-linear impacts are a major concern for management strategies due to their often surprising and potentially detrimental outcomes. Greater monitoring and research efforts are necessary to mitigate such 'ecological surprises' (Pansch and Hiebenthal, 2019; Kunze et al., 2021), through adequate identification and management of their underlying mechanisms.

Marine multiple stressor studies have increased over the last decade, focusing largely on cumulative climate impacts, generalised pollution, and fisheries (Bass et al., 2021). However, there remains a significant gap in upscaling research from single-species responses to population-, functional-group-, and ecosystem-level responses, particularly where stressors operate across different spatial scales (Cabral et al., 2019; Crain et al., 2008; Hoppit and Schmidt, 2022). While almost 75% of studies have shown that climate change intensifies the impacts of local stressors (Gissi et al., 2021), particularly at the species level, these findings lack consistent generalisability across higher levels of biological organisation and environmental context (Collins et al., 2023; Gissi et al., 2021; Turschwell et al., 2022). This highlights the need to consider local context dependence and ecosystem scale when interpreting research findings into practical management.

Rocky shores are particularly well suited to addressing these questions because they are tractable, experimentally accessible systems in which strong environmental variability, intense competition for space, and relatively rapid turnover, can reveal stressor effects across ecological levels (Hawkins et al., 2020, 2025; Kunze et al., 2021; Sanz-Lazaro et al., 2022). Intertidal organisms experience both marine immersion and aerial exposure, making them

useful for understanding how biological responses emerge under strongly fluctuating thermal, desiccation and hydrodynamic regimes across tidal zones (Helmuth et al., 2006; Kordas et al., 2015; Pansch and Hiebenthal, 2019). Moreover, understanding stressor-response dynamics in intertidal ecosystems is relevant beyond rocky shores as the land–sea interface links land-based nutrient and contaminant delivery, habitat connectivity and ecosystem services that support fisheries, water quality, recreation and shoreline protection (Fang et al., 2018; Singh et al., 2021).

Intertidal systems experience strong diurnal and seasonal variation in environmental parameters (Kunze et al., 2021). Their zonation reflects gradients in physiological tolerance and biotic interactions, while persistence under variable conditions is further shaped by physiological plasticity, ecological memory, generation time and dispersal (Mieszkowska et al., 2019). However, despite these adaptive capacities, this innately stressful and variable environment may compound the impacts of additional anthropogenic stressors. Climate-related drivers often operate across regional to global scales and are driven by processes beyond local management control. As a result, coastal management often focuses on more tangible local stressors such as water quality and land encroachment in isolation (Kunze et al., 2021; Wedding et al., 2022).

Combining local and global stressors is therefore especially important in coastal environments, where land-based pollution can modify how climatic stress is experienced and expressed. Treated and untreated sewage discharges from combined sewer overflows can increase nutrient and organic matter loading, contribute to eutrophication and oxygen depletion, and alter coastal trophic dynamics (Cabral-Oliveira et al., 2014; Giakoumis and Voulvoulis, 2023; Perry et al., 2024). In England, concern over such inputs has intensified in recent years owing to frequent storm-overflow releases and ageing or under-capacity wastewater infrastructure (Giakoumis and Voulvoulis, 2023; Perry et al., 2024). These local stressors, against a backdrop of global drivers like climate change, create complex interactions that require further research to understand their combined effects. There is a clear need to quantify multiple stressor impacts in a format that is applicable to policy and management, with a particular focus on coastal environments.

Stressor effects can differ markedly across biological levels, from gene expression and physiology, to populations, and ecological groups, even within the same system. Linking

multiple levels of biological organisation is critical for understanding how stressor effects emerge and propagate (Kong et al., 2025; Simmons et al., 2021). At the organismal level, stress responses can alter maintenance, growth, feeding, and reproduction; these changes can then influence abundance, trophic interactions and the relative dominance of ecological groups over time (Ames et al., 2020; Jackson et al., 2021). Yet, the vast majority of multiple stressor studies still focus on single response levels, limiting inference about how local and global drivers jointly influence organismal performance and higher-level ecological structure (Gissi et al., 2021; Orr et al., 2024; Turschwell et al., 2022).

The aim of this study was therefore to quantify the impacts of multiple stressors across levels of biological organisation in a rocky shore ecosystem, from gene expression and trophic biomarkers to population- and functional-group-level responses. To achieve this, an in situ warming experiment was installed across two rocky shore sites contrasting in ambient sewage-associated nutrient pollution. We evaluated the independent and interactive effects of warming and pollution on key biotic functional groups (barnacles, grazing gastropods, macroalgae, microphytobenthos) throughout a summer season. Barnacles were additionally employed as a model group to investigate population responses through body size, trophic ecology assessed using stable isotope analysis, and transcriptional state assessed using RNA-seq. Given their sessile nature and roles as abundant suspension feeders, dominant space occupiers and habitat-modifying intertidal organisms, barnacles serve as an ideal system for assessing whether stressor effects align or decouple across biological levels. The following a priori predictions were tested:

Predicted effects of warming

Warming is expected to negatively affect all sessile groups due to increased energetic demands and physiological strain (Bernatchez et al., 2019; Kordas et al., 2015), whereas effects on motile grazers occupying the plates may be weaker or more transient if movement reduces sustained exposure to warmed surfaces. Reduced grazing pressure may further benefit macroalgae through reduced herbivory (Kordas et al., 2015). Stable isotope signatures of barnacles are not expected to respond strongly to warming, given that the treatment is localised to the substrate and does not affect the water column and its food sources, although warming could still influence feeding behaviour or particle capture efficiency (Maar et al., 2024). We therefore expected any isotopic shifts associated with warming to be weaker than those driven by pollution-linked changes in food source or

availability. However, warming may impose physiological stress on barnacles, reflected by an increased elemental C:N mass ratio (i.e. the mass ratio of elemental carbon to nitrogen in tissues), indicating shifts in tissue composition under thermal stress (Zhang et al., 2018). At the transcriptional level, we expect warming to induce activation of cellular stress pathways and metabolic reallocation. Given the temperature contrast (see Methods) and exposure prior to sampling, any initial acute stress response is likely to be muted, with RNA-seq primarily capturing the longer-term, chronic transcriptional state (Collins et al., 2023; López-Maury et al., 2008; Zhan et al., 2019).

Predicted effects of pollution

Under the polluted site conditions, macroalgal cover is predicted to correlate positively with greater nutrient availability, in line with typical eutrophication trends, while simultaneously providing abundant food sources for grazing gastropods (Alestra & Schiel, 2015; Kordas et al., 2015). Polluted conditions may also trigger phytoplankton blooms, increasing food availability for sessile barnacles, which do not rely on local benthic primary productivity at the plate level (D'Costa et al., 2017). Elevated nutrients are expected to shift barnacle trophic dynamics, reflected by changes in stable isotope ratios that indicate alterations in the composition and source of available food (Laitano et al., 2018). At the transcriptional level, we expect nutrient enrichment (together with co-discharged contaminants associated with sewage inputs) to induce a broad response dominated by the upregulation of xenobiotic- and stress-response pathways, as well as metabolic processes reflecting higher energy intake (Balbi et al., 2021; Schaefer et al., 2022).

Predicted interactive effects of warming and pollution

We expect a net negative impact on macroalgae due to thermal stress, partly mitigated by pollution, as documented in previous studies (Borburema et al., 2020; Charan et al., 2022). Similarly, sessile barnacles may be negatively impacted by warming and its associated rise in metabolic demand, but this may be offset by increased food availability in polluted conditions. Functional groups may also benefit from removal of other groups, alleviating spatial competition (Crain et al., 2008; Harvey et al., 2013). Grazing gastropods may exploit abundant food (Kordas et al., 2015), but any interaction with warming may be dampened if grazers are not persistently exposed to the warmed plate surfaces due to their motility. Barnacle trophic indicators are expected to primarily reflect pollution-induced shifts in nutrient and food-web dynamics, with no additional impact from warming. At the

transcriptional level, we predict that combined warming and pollution will alter the magnitude and nature of pollution-induced responses, with upregulation of genes related to energy metabolism and ATP production and a relative downregulation of protein-folding pathways compared to warming alone, reflecting interaction effects on cellular energetics and proteostasis (i.e. maintenance of protein homeostasis) (Brasseur et al., 2022; Collins et al., 2023; Mohamed et al., 2014).

3.3 Materials and methods

3.3.1 Experimental design

We conducted our experiment in Peacehaven, East Sussex, England, on the open East Sussex coast of the eastern English Channel, within a wider hard-shore setting that includes intertidal chalk, rock, and mixed sediments (Sussex Inshore Fisheries and Conservation Authority, n.d.). Tides in this area are mixed semidiurnal, with a mean spring tidal range of ~6.3 m at nearby Newhaven (New Forest District Council (NFDC), 2017). The region is classified as Cfb (temperate oceanic climate; Köppen–Geiger classification), characterised by a maritime climate with a narrow annual temperature range. Such conditions make the region a useful system in which to investigate thermal stress on intertidal ecosystems. Regional forcing is typical of a moderately exposed English Channel coast, with waves approaching mainly from the south-west to west-south-west, and dominant net littoral transport directed from west to east (NFDC, 2017). These physical conditions support assemblages typical of Sussex rocky shores, with upper-shore lichen and *Pelvetia* zones, mid-shore mosaics of *Semibalanus balanoides* barnacles, herbivorous grazers including *Patella vulgata*, littorinid and trochid snails, and both *Fucus* and *Ulva* algal species, and lower-shore transitions toward *Fucus serratus* and red algal taxa. Regional habitat inventories and surveys indicate that Peacehaven and adjacent East Sussex hard shores are representative of the wider Sussex rocky shore fauna and flora (Sussex Wildlife Trust, n.d.). Peacehaven is also surrounded by multiple sewage outfalls operated by Southern Water (Fig. 1), with growing public concern surrounding pollution and water treatment misconduct (Cipirska, 2021; Department for Environment, Food, and Rural Affairs, 2023). Permission for installation was provided by Natural England and the Crown Estate.

We employed a fully factorial 2 × 2 experimental design with passively heated settlement plates in two sites with contrasting nutrient pollution levels. Friar's Bay (polluted site) lies immediately west of Newhaven Bay, downstream of several major sewage discharges: e.g. the Newhaven long-sea outfall (~2 km offshore to the SSE) and the Seaford storm overflow (~5.4 km to the east). By contrast, Bastion Steps (non-polluted site) is about 1.36 km to the west of these inputs and has no large outfalls nearby (the closest western outfall, Portobello Brighton No. 1, is ~3.2 km west of Bastion Steps, with infrequent discharge (Southern Water, n.d.)) (Fig. 1). Combined with predominantly eastward alongshore transport (tidal streams near Newhaven on spring tides reach ≈1.6 knots eastward flood vs. ≈1.1 knots westward ebb) and shore-normal waves from the S–SW (VisitMyHarbour, n.d.), this ensures effluent plumes are carried eastward along the Sussex coast (NFDC, 2017). Collectively, these factors supported our choice of installation sites, verified further by pre-installation nutrient verifications (see Supplementary Methods (Experimental) for additional details).

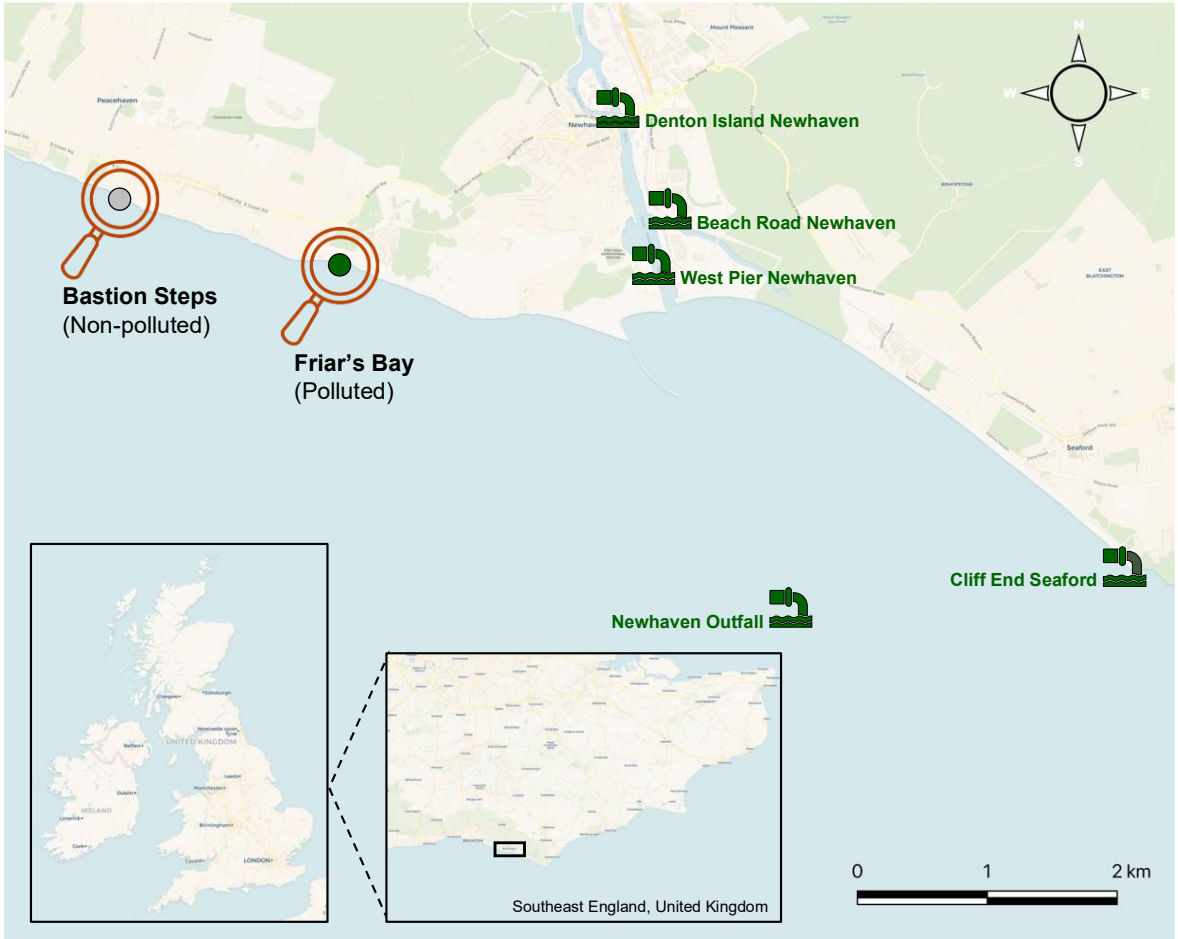


Figure 1 | Map of study area, showing settlement plate sites and local sewage outfalls. Map shows north arrow, with scale bar = 2 km. Bastion Steps (non-polluted: 50.789° N, −0.002° E) is indicated in grey, and Friar's Bay (polluted: 50.785° N, 0.021° E) is indicated in dark green. Principal sewage outfalls are indicated in dark green. Note that the illustrated major sewage inputs primarily lie east of Friar's Bay, whereas the western side has few active outlets (nearest western outfall, 'Portobello Brighton #1', is ~3.2 km from Bastion Steps).

To characterise the ambient nutrient context associated with site selection, we report pre-installation nutrient verification values from three paired excursions conducted before plate deployment (Table 1). These measurements were intended to verify a consistent contrast between the two selected shores, rather than a regulatory assessment of eutrophication status. Nitrate was measured using an ion-selective electrode (ISE) and is therefore interpreted cautiously in seawater, as chloride and matrix effects can bias absolute nitrate readings under saline conditions (see Supplementary Methods (Experimental)). Accordingly, nitrate values are presented here as raw instrument responses and are interpreted primarily as evidence of a repeated relative contrast between sites. Phosphate was measured photometrically and is reported as an absolute concentration. Across the three pre-installation excursions, the polluted site consistently showed a higher nitrate ISE response and higher phosphate than the non-polluted site (Table 2), supporting its designation as the more sewage-impacted site context used in the factorial design. At the regulatory scale, the surrounding Sussex coastal water body is currently classified as 'Good' for dissolved inorganic nitrogen (DIN) (Environment Agency, n.d.) under the Water Framework Directive (Department for Environment, Food & Rural Affairs (DEFRA), (2009)) where coastal nutrient status is assessed using winter mean DIN rather than short-term spot nitrate measurements (OSPAR Commission, 2022). Moreover, although the wider Sussex coastal water body is classified as 'Good' for winter DIN under the WFD, this does not preclude seasonal nutrient drawdown or fine-scale enrichment pulses at particular shores; indeed, English Channel time-series show that nitrate is commonly depleted during the stratified summer period, when nutrient availability can approach limiting levels in surface waters (McEvoy et al., 2023).

To create our warming condition, we constructed 12 control (white) and 12 warmed (black) plates (Figs. 1A and B), inspired by Kordas et al. (2015), with colour ensuring a categorical difference in thermal absorption when installed at mid-tide (Fig. 1C; Table 2), as shown in similar studies (Kordas et al., 2015; Kordas & Harley, 2016; Lathlean & Minchinton, 2012). A full instructional document for plate construction is provided in the SI. Six black and six white plates were deployed in each site (polluted vs. non-polluted). The polluted site had significantly elevated levels of both dissolved inorganic nitrate (NO^{3-}) and dissolved inorganic phosphate (PO_4^{3-}) prior to plate deployment (Fig. 1D; Table 1; see also SI Fig. S1 for verifications during the experimental period). Because only one site represented each pollution context, pollution is interpreted here as a site-level contrast in ambient sewage-associated nutrient conditions rather than as a spatially replicated pollution treatment.

Each plate was topped with a 9 cm × 9 cm textured epoxy settlement area, mimicking natural rocky substrate for recruitment (Kordas et al., 2015). All plates were installed at mid-tide (established via typical biotic zonation cues and local tidal height markers), standardising aerial exposure which drives the daily warming difference. Plates were mounted horizontally, with the settlement surface facing upward, on near-horizontal substrata at both sites. To record settlement temperature, ElectricBlue EnvLoggers were embedded within the plates in direct contact with the epoxy, recording temperature every 90 min (0.1°C resolution) (Fig. 1A). Plates were installed in January 2023 and left in place until June 2023 to permit field establishment of naturally recruiting assemblages under continuous treatment exposure before repeated summer surveys, after which seven fortnightly surveys were conducted from June–September 2023, following similar in situ schedules (Kordas et al., 2015; Kordas & Harley, 2016). Full information on temperature monitoring, settlement plate design and nutrient quantification prior to and during the experimental period is provided in the SI (Supplementary Methods (Experimental)).

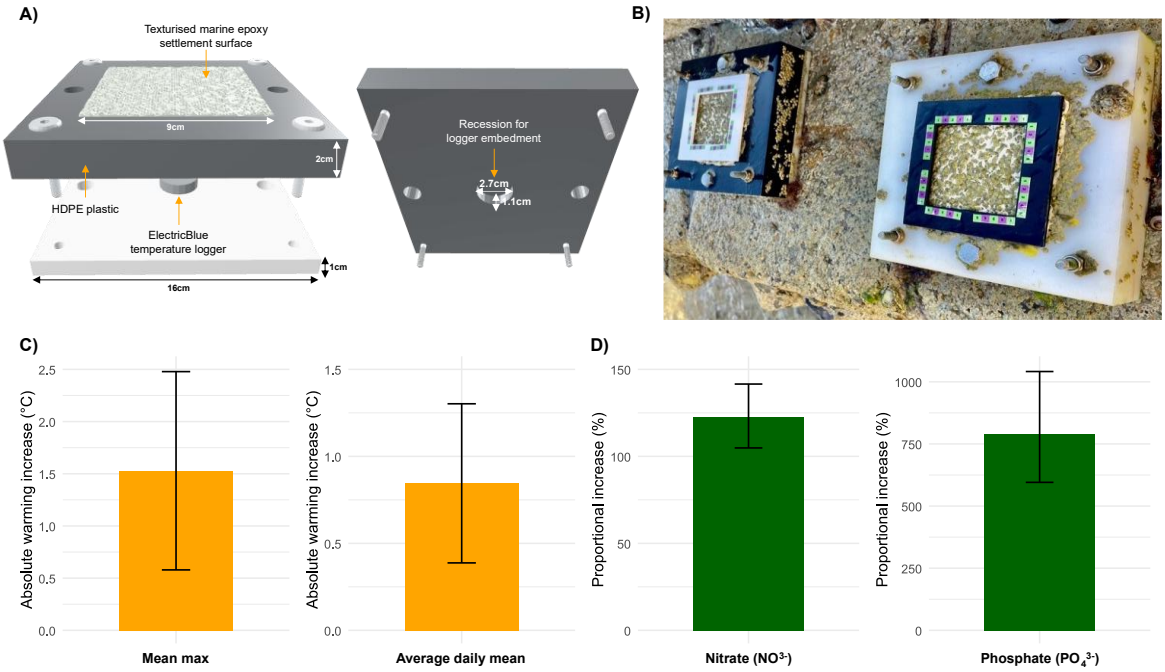


Figure 2 | Summary figure of methodology. A) 3D rendering of the black (warmed) treatment plate, showing the epoxy settlement surface on the left and the underside of the top plate with recession for installation of the temperature logger on the right. B) 3D-printed 40% opening sampling stencil, shown here on developed black and white plates, with 2.5 cm scale bars applied for barnacle size measurement calibration. C) Absolute warming increases (°C), shown as two separate warming metrics: Mean maximum temperature and tide-adjusted average daily mean for the warmed treatment relative to the ambient control (ΔT = Warmed − Ambient), recorded and averaged across all mid-tide plates during the experimental period (n = 12 warmed plates; n = 12 ambient plates; see SI for full warming verification). Error bars show 95% confidence intervals for ΔT, based on the difference between independent treatment means, with uncertainty propagated from the two groups' standard errors. D) Proportional increase (%) in mean verification values of nitrate and phosphate at the polluted site relative to the non-polluted control, based on three paired pre-installation verification excursions (n = 3 paired excursions; each excursion based on the mean of three water samples per site, i.e. 9 raw samples per site overall). Nitrate and phosphate are shown in separate subpanels with independent y-axis scales, because these metrics differ markedly in magnitude; bar heights should therefore be interpreted relative to the axis within each subpanel rather than compared directly between nutrients. For nitrate, absolute concentrations are not reported because the in situ ion-selective electrode (ISE) was affected by chloride in seawater; we therefore show proportional elevation under matched PSU (salinity) between sites (see SI). Phosphate is shown in the same way for comparability, and its absolute verification values are provided in Table 1.

Month	Site	Nitrate ISE readings (NO^{3-} mg/L, uncorrected)	PO_4^{3-} readings (mg/L)
September 2022	Polluted	61.2; 60.1; 56.8 ($\bar{x}$ = **59.37**)	0.12; 0.10; 0.10 ($\bar{x}$ = **0.110**)
	Non-polluted	24.8; 29.9; 28.8 ($\bar{x}$ = **27.83**)	0.00; 0.00; 0.00 ($\bar{x}$ = **0.000**)
October 2022	Polluted	66.0; 64.8; 65.0 ($\bar{x}$ = **65.27**)	0.10; 0.06; 0.18 ($\bar{x}$ = **0.113**)
	Non-polluted	28.9; 34.7; 30.1 ($\bar{x}$ = **31.23**)	0.00; 0.01; 0.00 ($\bar{x}$ = **0.003**)
November 2022	Polluted	68.1; 65.1; 62.2 ($\bar{x}$ = **65.13**)	0.20; 0.11; 0.12 ($\bar{x}$ = **0.143**)
	Non-polluted	37.7; 32.1; 30.3 ($\bar{x}$ = **33.37**)	0.00; 0.00; 0.00 ($\bar{x}$ = **0.000**)

Table 1 | Pre-installation nutrient verification readings used for site selection. Three paired verification excursions were conducted before plate installation (September–November 2022). At each date and site, three water samples were taken and averaged. Nitrate values are shown as raw ion-selective electrode (ISE) readings (NO^{3-} mg/L, uncorrected) and are included only as the instrument response used to verify a repeated relative contrast between sites; they are not interpreted as absolute seawater nitrate concentrations because of chloride interference (see Supplementary Methods (Experimental)). Phosphate values were obtained by photometric assay and are reported as absolute concentrations (PO_4^{3-}). This table is therefore presented as site-context verification rather than as a regulatory classification metric.

Treatment	Mean max. (raw): Installation and sampling	Mean ADM: Installation and sampling	Mean ADM: Sampling only	Tide-adjusted mean ADM: Sampling only
Black	38.0	17.6	25.5	29.5
White	36.4	17.4	25.2	28.7

Table 2 | Summary of recorded plate temperatures. Mean max represents the maximum values ever recorded by plate loggers, averaged across all replicates in each warming group. Mean average daily max (ADM) values were calculated by using the residual of the ADM for each plate logger from the grand mean on each sampling date, subsequently averaged across all replicates in each warming group. This was further tide-adjusted by only including days in which low tide occurred during peak daytime hours (defined for simplicity here as 10:00–14:00), thereby maximising exposure and thermal absorption (see Supplementary Methods (Experiential)).

3.3.2 Sampling

At each of the seven sampling dates, we quantified four functional-group responses on settlement areas: 1) barnacle abundance; 2) grazing gastropod abundance; 3) macroalgal cover; and 4) microphytobenthos concentration (cyanobacteria, diatoms, green microalgae). Data were obtained via *in situ* counts/assessments and photo-based analyses, allowing sampling under time-limited tidal windows (see SI Table S1 for a list of the main taxa or genera representing each functional group expected and observed at these sites).

Season-wide functional-group/population responses

For barnacle abundance, populations were subsampled using a stencil with a 40% opening (Fig. 1B), to discount edge effects. Photographs were then analysed using a machine-learning model produced by the mobile application 'CountThings', which employs convolutional neural networks (CNNs) alongside specialised one-stage, two-stage, keypoint-based, and transformer-based frameworks for robust object detection. The model was trained on marked field-establishment images and distinguished live barnacles via intact opercula (see Supplementary Methods (Experimental) for further details on CountThings architecture and settings). Sampling stencils contained a 25 mm scale bar used to calibrate barnacle body size measurements in ImageJ (Fig. 1B). Images were overlaid with a 10 × 10 grid, and 10 random coordinates were drawn; at each coordinate, the upper-leftmost barnacle was

measured across the maximum rostro-carinal axis following previous methods employed as a non-destructive, allometric proxy (Ten et al., 2019). New images were taken for macroalgal coverage analyses without a stencil. Colour thresholding metrics were applied in ImageJ (RGB: Red: 0–50; Green: 0–250; Blue: 0–50), maximising green pigments whilst minimising hues from invertebrates and epoxy. Herbivorous gastropods present on each plate (littorinid, trochid, patellid snails) were counted manually in situ during each survey. Predatory whelks (e.g. *Nucella*) were not observed in our sampling assemblage.

For microphytobenthos, a BenthoTorch (bbe Moldaenke) was used on each plate. The BenthoTorch permits rapid quantification of diatoms, green microalgae, and cyanobacteria through excitation of each group's characteristic fluorescence profile (chl-a/cm^2). Plates were shaded for 30 min before measurement to stabilise light-driven variation in chlorophyll-a (Kaylor et al., 2018). Because these group-specific estimates were resolved simultaneously from the same *in situ* fluorescence measurement on each plate, they represent linked components of a single plate-level microphytobenthos reading rather than independent samples.

End-of-summer responses: barnacles

At the end of summer, two barnacles of the same species (*Semibalanus balanoides*) per settlement plate were randomly selected for stable isotope analysis (SIA). Internal tissues were scraped into 1.5 mL microcentrifuge tubes (48 samples), dried at 60 °C for 48 h, and weighed. Tissues were then pooled by plate into 24 composite samples ($n = 6$ per treatment; two samples below the recommended ≥ 0.7 mg threshold for laboratory analyses). Samples were analysed using a SerCon Callisto CF-IRMS system to obtain $\delta^{13}C$ (Vienna Pee Dee Belemnite standard) and $\delta^{15}N$ (atmospheric N_2 standard) values, from which elemental C:N ratios were derived. Intermittent runs of calibration standards (seal collagen, alanine, and IAEA-CH-6 (sucrose)) provided continuous drift correction and verified instrument performance, with seal collagen and alanine chosen for their stable, well-characterised isotopic compositions and IAEA-CH-6 serving as an additional $\delta^{13}C$ standard.

For barnacle gene expression analyses, two barnacles were similarly selected per plate at the end of summer for RNA sequencing (RNA-seq), and preserved in RNAlater solution (Invitrogen) according to the manufacturer's instructions. This end-of-summer sampling was intended to characterise the integrated late-season transcriptional state after repeated

treatment exposure, rather than an acute response to a single emersion event (see Supplementary Methods (Experimental)). Samples stored in RNAlater were rinsed in phosphate-buffered saline (PBS) to remove precipitated salts, and RNA was then isolated from individual barnacles using an RNeasy Micro Kit (Qiagen, Hilden, Germany), according to the manufacturer's instructions. RNA quantity, purity and integrity were assessed using an Agilent 5400 Bioanalyzer. Samples with an RNA Integrity Number (RIN) > 5, indicating suitably low degradation for laboratory analyses ($n = 8$ for ambient × polluted/non-polluted; $n = 7$ for warmed × polluted/non-polluted), were subjected to RNA-seq on one lane of an Illumina NovaSeq X Series (paired-end (PE) 150 bp) by Novogene, Cambridge, UK. Assembly was performed by Novogene, with subsequent bioinformatics analyses performed in-house.

3.3.3 Statistical analyses

Statistical analyses of ecological data were run in R version 4.4.3.

Season-wide functional-group/population responses

To evaluate the independent and interactive effects of warming and nutrient pollution, we used two modelling approaches. For each sampling date, generalised linear models (GLMs) with appropriate families and links were fitted for each response (model specifications and diagnostics summarised in SI Table S2). Additionally, to capture season-long trends in stressor interactions and responses, generalised additive mixed models (GAMMs) were constructed for every response variable. In all models, warming treatment and pollution context (i.e. the two site contexts) were treated as fixed categorical predictors; because only one shore represented each pollution context, site was not modelled as a random effect. Each GAMM incorporated smooth terms for time (days since the start of summer), allowed interactions with these categorical stressor variables, and included plate identity as a random effect to account for repeated measures of the same settlement plate across sampling dates (see Supplementary Methods (Analyses)). GAMMs are widely used to model non-linear temporal trends in ecological time series, including irregularly spaced observations and seasonal trajectories (Pedersen et al., 2019; Simpson, 2018; Wood, 2025). Diagnostics confirmed residual normality and homoscedasticity. Notably, for grazers, data were aggregated to binary presence/absence (i.e. occurrence) to improve GLM and GAMM model convergence, given the high frequency of zero counts and separation issues; resulting log-odds models are thus interpreted as the probability of grazer presence in a given treatment

(see Supplementary Methods (Analyses)). Furthermore, conditional plots were constructed for all GLMs to visualise effect modification and asymmetry in interactions, showing directly whether the effect of warming differed between pollution treatment sites on each sampling date, as recommended for detecting and interpreting interactive ecological responses (Spake et al., 2023). Full details on GLM/GAMM model choices, diagnostics, and conditional plots are provided in the SI (Supplementary Methods (Analyses); Table S2; Figs. S2–S8).

To classify interaction effects, we extracted the relevant coefficient estimates from our GLM and GAMM models and interpreted the fitted regression interaction as a departure from a null model of independent stressor effects on the model's link scale (Madge Pimentel et al., 2025). Each model's linear predictor comprises the intercept (a), the main effect coefficients for warming (β(w)) and pollution (β(p)) and an interaction term (β(int)). We define the 'additive' expectation (i.e. the null model on a given model's link scale) as the sum of the main effect coefficients ($\Delta add = \beta(w) + \beta(p)$). We then define the observed change including the interaction ($\Delta obs = \Delta add + \beta(int)$), where Δobs represents the total predicted change when the interaction between warming and pollution is accounted for. An interaction coefficient of zero indicates that the observed response matches this null expectation, whereas any deviation ($\beta(int) \neq 0$) quantifies how much the combined effect diverges from this. Notably, because 'additivity' is scale-dependent, interaction classifications are specific to the link function used (Madge Pimentel et al., 2025; Spake et al., 2023). Moreover, we note that such interactions are statistical (effect modification in the fitted model), and do not definitively demonstrate unique mechanistic interactions between stressors (Orr et al., 2024; Schäfer et al., 2023; Spake et al., 2023); we therefore interpret interaction types cautiously and in the context of biological plausibility and experimental design. For interpretive clarity, the interaction term therefore indicates whether the effect of warming was stronger, weaker, or directionally altered at the polluted site relative to the null expectation from the main effects alone.

The interpretation of the statistical interaction term is contextualised by the direction of the independent effects. If both stressor effects are positive, a positive interaction term indicates that the observed effect exceeds the additive expectation (synergism), while a negative interaction indicates antagonism. Similarly, if both stressors are negative, a negative interaction term signifies that the combined negative impact is more severe than predicted (synergism in the negative direction), whereas a positive interaction term indicates

antagonism. For stressors with opposing effects, if the interaction term shares the same direction sign as the additive expectation, the interaction reinforces the net effect (synergism relative to additivity). Whereas, if the interaction is of the opposite sign, it counteracts the net effect (antagonism). We further include the concept of a reversal (Jackson et al., 2016). A reversal occurs when the interaction term flips the overall direction of the response relative to the null expectation. For example, if both independent stressors are negative (predicting a net decrease) but the inclusion of a positive interaction term results in an overall positive response, this constitutes a reversal, and vice versa in the opposite conditions.

We further contextualised interactions using a confidence interval-based, smallest effect size of interest (SESOI) comparison, grounded in equivalence-testing logic (Lakens, 2017). For models with log or logit links, additivity is defined on the link scale; after back-transformation, this corresponds to $\exp(\beta(\text{int})) = 1$, where $\exp(\beta(\text{int}))$ is an interaction ratio that quantifies the multiplicative deviation of the combined effect from the additive expectation on the link scale (for log links, a multiplicative deviation on the response scale; for logit links, a ratio of odds ratios). We employed an SESOI band of ±5% around the null (±5% on the raw identity scale; 0.95–1.05 on the $\exp(\beta(\text{int}))$ scale for log and logit models) as a qualitative flag for relatively mild departures from additivity. Accordingly, when an interaction was statistically supported ($p < 0.05$), we retain its directional interaction classification, but explicitly acknowledge if the 95% CI of the interaction term overlapped this ±5% band, noting it as a mild deviation from the null model.

End-of-summer responses: barnacles

Barnacle stable isotope responses were analysed once at the end of summer. Here, we modelled $\delta^{13}C$, $\delta^{15}N$, and elemental C:N mass ratio using two-way factorial ANOVAs with fixed effects of pollution (non-polluted vs. polluted), warming (ambient vs. warmed), and their interaction. We report full *F*-statistics, degrees of freedom, and *p*-values for both main and interaction terms.

For barnacle transcriptomic responses, sequencing produced ~998 million 'clean' reads (i.e. adaptors and low-quality reads removed, leaving 19.5–56.2 million reads per sample), assembled into 376,108 contigs (145,062 putative genes) using Trinity v2.15.1 (Haas et al., 2013). Transcripts were annotated using the Trinotate v4.0.2 pipeline, performing BLASTx/BLASTp searches against the Swiss-Prot and Gene Ontology (GO) databases with

default parameters. To quantify gene expression, reads were aligned to the assembled transcriptome using Salmon v1.10.0 (Patro et al., 2017) with default parameters. All downstream analyses were performed in R v4.4.2. Counts were imported into R using tximport v1.34.0 (Patro et al., 2017) and differential expression was performed using DESeq2 v1.46.0 (Soneson et al., 2016). After removal of low-count genes (< 10 total counts), 122,570 genes were included. The model (~ Pollution + Warming + Pollution:Warming) allowed identification of significantly differentially expressed genes (DEGs, $p_{adj} < 0.05$) in response to independent warming, independent pollution, and their interaction (i.e. genes whose response to warming differed between pollution conditions). For significantly interactive genes, we characterised synergisms, antagonisms, and reversals as described for the ecological data. To identify affected biological pathways, we tested DEGs for gene ontology (GO) term enrichment using goseq v1.58.0 (Young et al., 2010).

3.4 Results

3.4.1 Invertebrate responses

Barnacle abundance

GLMs showed that barnacle abundance was consistently lower on warmed plates and higher at the polluted site across sampling dates. For example, in June, warming significantly reduced barnacle abundance ($\beta = -0.693$, SE = 0.149, $p < 0.001$), while abundance was higher at the polluted site ($\beta = 2.087$, SE = 0.120, $p < 0.001$). Moreover, a positive interaction term was evident ($\beta = 0.414$, SE = 0.182, $p = 0.023$) which, when exponentiated, corresponds to a ≈51% increase relative to the multiplicative null model (Fig. 3A; SI Table S3). In direct terms, this positive interaction indicates that the negative effect of warming was weaker at the polluted site than at the non-polluted site (equivalently, the positive site contrast was larger under warming). Notably, the positive interaction effect size on all dates remained smaller than the individual positive effect of pollution, which was the primary driver of abundance (SI Table S3). Because the additive expectation on the model (log) scale was positive on every date ($\Delta add = \beta(w) + \beta(p) > 0$), the consistently positive interaction terms indicate amplification of that expected increase ($\Delta obs > \Delta add$), and were therefore classified as synergistic deviations from the multiplicative null model on six of seven dates (+51% to

+74%; SI Table S3; Fig. S2). Whole-summer GAMM predictions mirrored the discrete-time GLM results: barnacle abundance was elevated at the polluted site ($\beta = 2.087$, SE = 0.210, $p < 0.001$), while warming suppressed abundance ($\beta = -0.887$, SE = 0.214, $p < 0.001$). The interaction term was positive ($\beta = 0.507$, SE = 0.299, $p = 0.090$), indicating near-significant synergistic effects. However, the 95% CI (0.924–2.984) overlaps our ±5% SESOI band (0.95–1.05); we therefore interpret the season-wide pattern as a mild synergism. Additionally, GAMM smooth terms indicated treatment-specific temporal structure in warmed treatments, with approximately linear time trends (edf ≈ 1) in the non-polluted condition (edf = 1; $p = 0.048$), and a non-linear temporal pattern in the polluted condition (edf = 1.802, $p < 0.001$), whereas the remaining conditions showed no detectable temporal pattern (SI Table S10; Fig. S9A).

Barnacle size

GLMs showed no significant effect of warming on barnacle body size on any date, whereas barnacles were significantly larger at the polluted site on July 1 ($\beta = 0.362$, SE = 0.140, $p = 0.017$) and July 2 ($\beta = 0.414$, SE = 0.154, $p = 0.014$) (Fig. 3B; SI Table S4). The interaction term was neither significant nor directionally consistent across dates (SI Table S4; Fig. S3). The whole-season GAMM (adjusted $R^2 = 0.629$) similarly showed no significance of parametric stressor terms at the season-wide scale. However, the GAMM was dominated by significant temporal trends within treatments, with approximately linear increases in both non-polluted treatments (Ambient: edf = 1.000, $p < 0.001$; Warmed: edf = 1.000, $p < 0.001$) and non-linear trajectories in polluted conditions (Ambient: edf = 5.186, $p < 0.001$; Warmed: edf = 3.965, $p < 0.001$) (SI Table S11; Fig. S9B).

Grazer occurrence

Bias-reduced logistic GLMs indicated no independent effect of warming on grazer occurrence (log-odds scale; interpreted as probability of presence) across dates. Grazer occurrence was, however, higher at the polluted site on two dates (June: $\beta = 3.860$, SE = 1.870, $p = 0.039$; the same effect was observed on July 2) (Fig. 3C; SI Table S5). Interaction terms across all dates were neither consistent nor significant (SI Table S5; Fig. S4). Whole-summer GAMM predictions (adjusted $R^2 = 0.602$) mirrored the GLMs: occurrence was higher at the polluted site ($\beta = 2.865$, SE = 0.768, $p < 0.001$), warming was non-significant ($\beta = -1.640$, SE = 1.225, $p = 0.181$) and the interaction was also non-significant ($\beta = 3.737$, SE = 2.597, $p = 0.150$). Temporal trends varied by treatment

combination, with significant smoothing terms in the ambient, non-polluted condition (edf = 0.790, $p = 0.050$) and the warmed, non-polluted condition (edf = 3.517, $p = 0.024$) (SI Table S12; Fig. S9C).

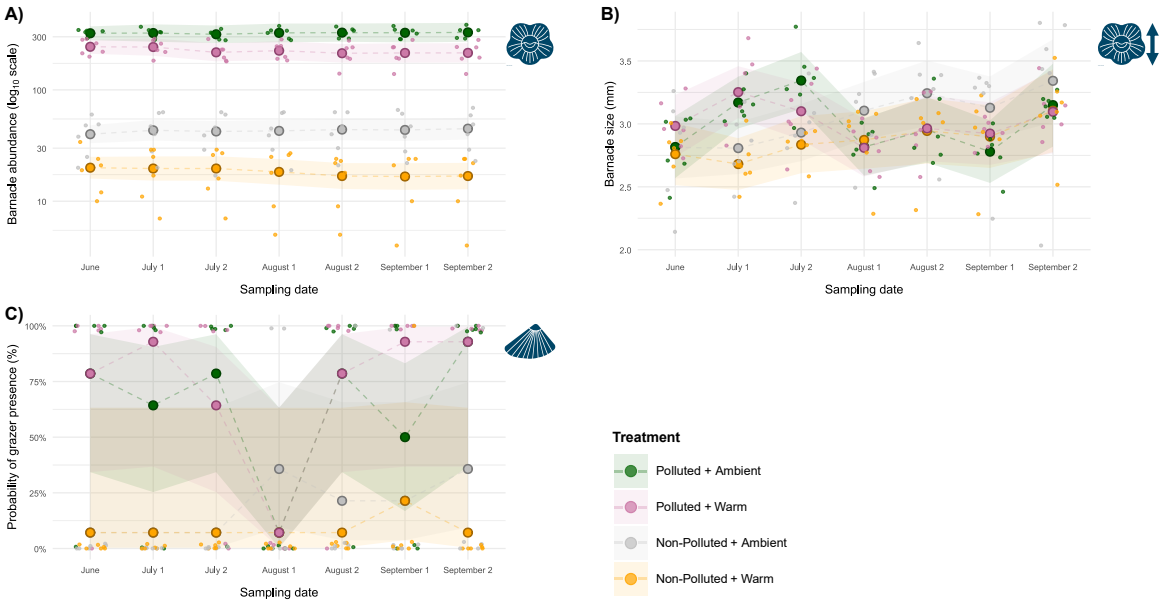


Figure 3 | Invertebrate responses to warming across polluted and non-polluted sites on each sampling date. Large circles show GLM model-estimated treatment means for each sampling date; semi-transparent ribbons show 95% confidence intervals around those date-specific estimates, with illustrative dashed connectors between treatment means (whole-season temporal trends are evaluated with GAMMs; see SI Figure SS9A–C for GAMM temporal visualisations). Smaller points are jittered raw replicate values to illustrate distributions around each estimated mean response. A) Barnacle abundance (log_{10} axis). B) Barnacle body size (mm). C) Grazer occurrence (predicted probability of presence). Full model specifications and diagnostics are provided in the SI (Table S2).

Barnacle stable isotope composition

End-of-summer stable isotope analyses showed site-associated differences in $\delta^{13}C$ and $\delta^{15}N$ driven primarily by pollution, whereas elemental C:N mass ratio was influenced by warming (Fig. 4). The polluted-site contrast was associated with lower barnacle $\delta^{15}N$, from approximately 11.67‰ in the non-polluted site to 11.33‰ at the polluted site ($F_{1,18} = 6.81$, $p = 0.017$). Neither warming nor its interaction with pollution had a discernible effect on $\delta^{15}N$ ($p = 0.975$ and $p = 0.546$, respectively). Similarly, barnacles at the polluted site also exhibited more negative $\delta^{13}C$, shifting from around −17.24‰ in the non-polluted site to −18.37‰ at the polluted site ($F_{1,18} = 64.90$, $p < 0.001$), with no significant effect of warming or the interaction ($p = 0.890$ and $p = 0.772$, respectively). In contrast, the elemental C:N ratio was unaffected by pollution ($p = 0.746$) but increased significantly under warming, rising from ~4.12 (ambient) to ~4.22 (warmed) ($F_{1,18} = 5.33$, $p = 0.033$). Full group means and ANOVA outputs are provided in the SI (Tables S16 and S17).

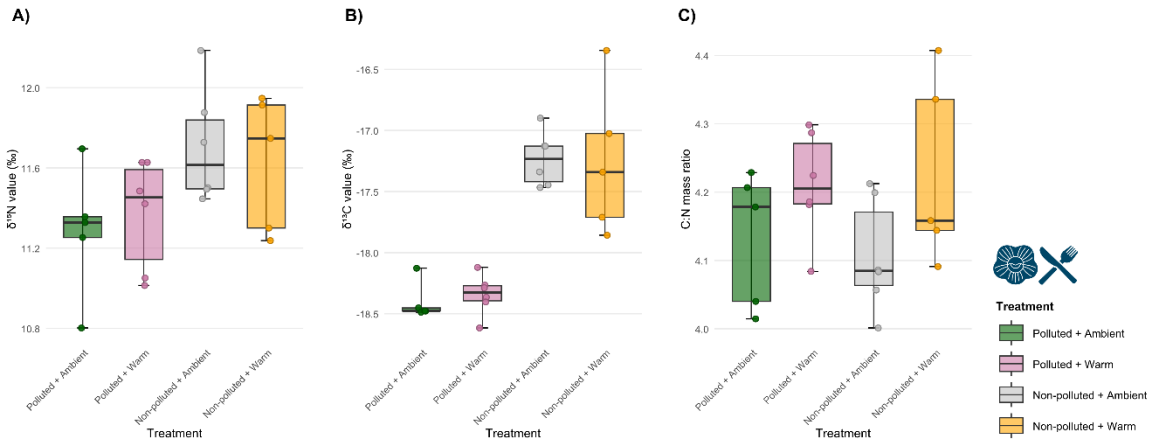


Figure 4 | Barnacle stable isotope compositions at the end-of-summer sampling period (September 2). Boxes show the interquartile range (IQR), with the horizontal line indicating the median. Given the small sample size per treatment (n = 5–6), whiskers are shown to the minimum and maximum observed values within each treatment to aid visual interpretation, while individual points show all raw replicate values. A) $\delta^{15}N$ values (‰). B) $\delta^{13}C$ values (‰). C) Elemental C:N mass ratio. Additional summary statistics and analytical standards outputs are provided in the SI (Tables S16 & S17).

Barnacle transcriptional responses

Exposure to warming alone induced a relatively weak transcriptomic response, significantly affecting the expression of 471 genes ($p_{adj} < 0.05$), of which nearly 80% were downregulated (372 genes) and significantly enriched for cytoskeletal and structural (cilium-associated) proteins (Fig. 5A). In contrast, the polluted site was associated with a much stronger transcriptomic response, with significant changes in the expression of 4,787 genes including 3656 upregulated genes (76%), largely associated with protein turnover and DNA repair. At the polluted site, downregulated genes were dominated by GO terms involved in protein folding (i.e. chaperone and proteostasis pathways; Fig. 5B). There was a significant interactive effect of warming and pollution on the expression of 316 genes (Fig. 5C). Reversals were the dominant interaction type by frequency (~62% of DEGs), followed by antagonisms (~29%) and limited synergisms (~9%). For antagonistic interactions, only downregulated genes displayed functional enrichment, with two GO terms significantly involved in electron/proton transport (e.g. COX genes). Synergistic upregulated genes showed no functional enrichment, whereas downregulated genes were significantly enriched for multiple protein folding GO terms. Within chaperone-mediated protein folding (GO:0061077), five putative heat-shock proteins (HSP) genes showed no significant induction in response to warming alone ($p_{adj} > 0.05$), but a significant downregulation in response to pollution ($p_{adj} < 0.05$), which was reinforced by their interaction (Fig. 5C). No reversals showed any significant functional enrichment. Full DEG-level outputs (log_2FC, significance, database

hits, interaction classifications) and GO enrichment outputs for all contrasts are provided in the accompanying workbooks, archived with the project data and code repository (see Data Availability).

Figure 5 | Barnacle transcriptomic responses at end-of-summer sampling period (September 2). Top enriched biological process (BP) Gene Ontology (GO) terms for individual genes significantly affected ($p_{adj} < 0.05$) by: A) the main effect of warming; B) the main effect of pollution; and C) the warming × pollution interaction. Across all panels, arrows indicate the number and direction (up/downregulation) of differentially expressed individual genes, with 'n.s.' denoting cases where no collective GO term was significantly enriched ($p_{adj} > 0.05$), and bar plots showing top enriched GO terms for a given direction. In panel C (left), we show the classification of interaction types for genes with a significant interactive response (+/− indicating up- or downregulation respectively): (A+ = antagonistic positive; A− = antagonistic negative; S+ = synergistic positive; S− = synergistic negative; R+/− = reversal from positive to negative; R−/+ = reversal from negative to positive). The middle panel shows significant BP GO term enrichments for negative synergisms specifically, and the right panel shows mean ± SE $\log_2$ fold-change (FC) for individual genes within the top enriched BP GO term of these negative synergisms (GO term: Chaperone-mediated protein folding; five HSP genes and one endoplasmic reticulum (ER) chaperone).

3.4.2 Algal responses

Macroalgal cover

GLMs showed that macroalgal cover was higher at the polluted site on most dates, significantly so on all sampling dates from August 1 onwards (β ranging from 1.263 to 1.596, all $p < 0.001$). In contrast, warming tended to reduce cover with near-significant effects ($0.05 \leq p < 0.10$) observed in the latter half of the season (August 1, September 1, September 2; β ranging from −0.795 to −0.754) (Fig. 6A; SI Table S6). The interaction between warming and pollution was neither significant nor consistent across dates (SI Table S6; Fig. S5). Whole-season GAMM predictions (adjusted $R^2 = 0.655$) corroborated the dominant seasonal pattern of higher macroalgal cover under pollution and lower cover under

warming, with both main effects statistically significant (warming: $\beta = -0.608$, SE = 0.297, $p = 0.041$; pollution: $\beta = 0.632$, SE = 0.285, $p = 0.027$), while the interaction remained non-significant ($\beta = 0.317$, SE = 0.410, $p = 0.439$) (SI Table S13; Fig. S9D). Smooth terms were strongly significant across all treatments (all $p < 0.001$), with edf values (ranging from 2.451 to 4.102) indicating non-linear seasonal fluctuations in each treatment combination (SI Table S13).

Cyanobacteria concentration

GLMs indicated that cyanobacteria concentration was higher at the polluted site on all dates from July 1 onwards, whereas warming showed no statistical significance (Fig. 6B; SI Table S7). Significant positive interactions were observed in June ($\beta = 0.057$, SE = 0.027, $p = 0.047$) and July 2 ($\beta = 0.175$, SE = 0.080, $p = 0.040$), denoting synergistic effects on both dates (SI Table S7; Fig. S6). In direct terms, these interactions indicate that cyanobacteria concentrations were higher than expected under the combined treatment on those dates; equivalently, the polluted-site contrast was larger under warming on those dates. GAMM predictions (adjusted $R^2 = 0.637$) supported these findings: elevated seasonal concentration at the polluted site ($\beta = 0.268$, SE = 0.026, $p < 0.001$), whereas warming was non-significant ($\beta = -0.011$, SE = 0.009, $p = 0.188$). Here, the interaction was positive and statistically significant ($\beta = 0.086$, SE = 0.039, $p = 0.030$), indicating a synergistic effect. However, the 95% CI overlaps our ±5% SESOI band (identity scale band = ±0.016; CI = [0.009, 0.162]); we therefore interpret this season-wide pattern as a mild synergism (SI Table S14; Fig. S9E). Smooth-term results indicated significant seasonal variation across all four treatment combinations (SI Table S14).

Diatom concentration

Diatom concentration similarly reflected these patterns. GLMs showed that diatom concentration was positively and significantly influenced by pollution on the majority of dates, whereas warming only showed a significant negative effect on August 1 ($\beta = -0.063$, SE = 0.028, $p = 0.033$) (Fig. 6C; SI Table S8). The interaction was inconsistent and insignificant across all sampling dates (SI Table S8; Fig. S7). GAMM predictions (adjusted $R^2 = 0.779$) supported a positive pollution effect ($\beta = 0.230$, SE = 0.047, $p < 0.001$), with warming remaining non-significant ($\beta = -0.004$, SE = 0.047, $p = 0.927$). The interaction term similarly remained non-significant ($\beta = -0.003$, SE = 0.066, $p = 0.963$) (SI Table S15; Fig. S9F). Smooth term analysis indicated that temporal trends were highly significant at the

polluted site (Ambient, polluted: edf = 5.777, $p < 0.001$; Warmed, polluted: edf = 5.818, $p < 0.001$), but were non-significant in the non-polluted site (SI Table S15).

Green microalgae concentration

For green microalgae, only the June data provided sufficient variation to fit a GLM; on all subsequent sampling dates, concentrations were essentially zero. In June, the GLM indicated that green microalgae concentration was significantly higher at the polluted site ($\beta = 0.098$, SE = 0.028, $p = 0.002$). Similarly, the effect of warming also showed a positive association ($\beta = 0.045$, SE = 0.023, $p = 0.062$) (Fig. 6D; SI Table S9). The interaction between warming and pollution was statistically insignificant (SI Table S9; Fig. S8). Given near-zero concentrations after June, no further GLMs or time-series GAMM analyses were performed. Later time points are presented descriptively with raw data and means alongside the June GLM model predictions in Fig. 6D.

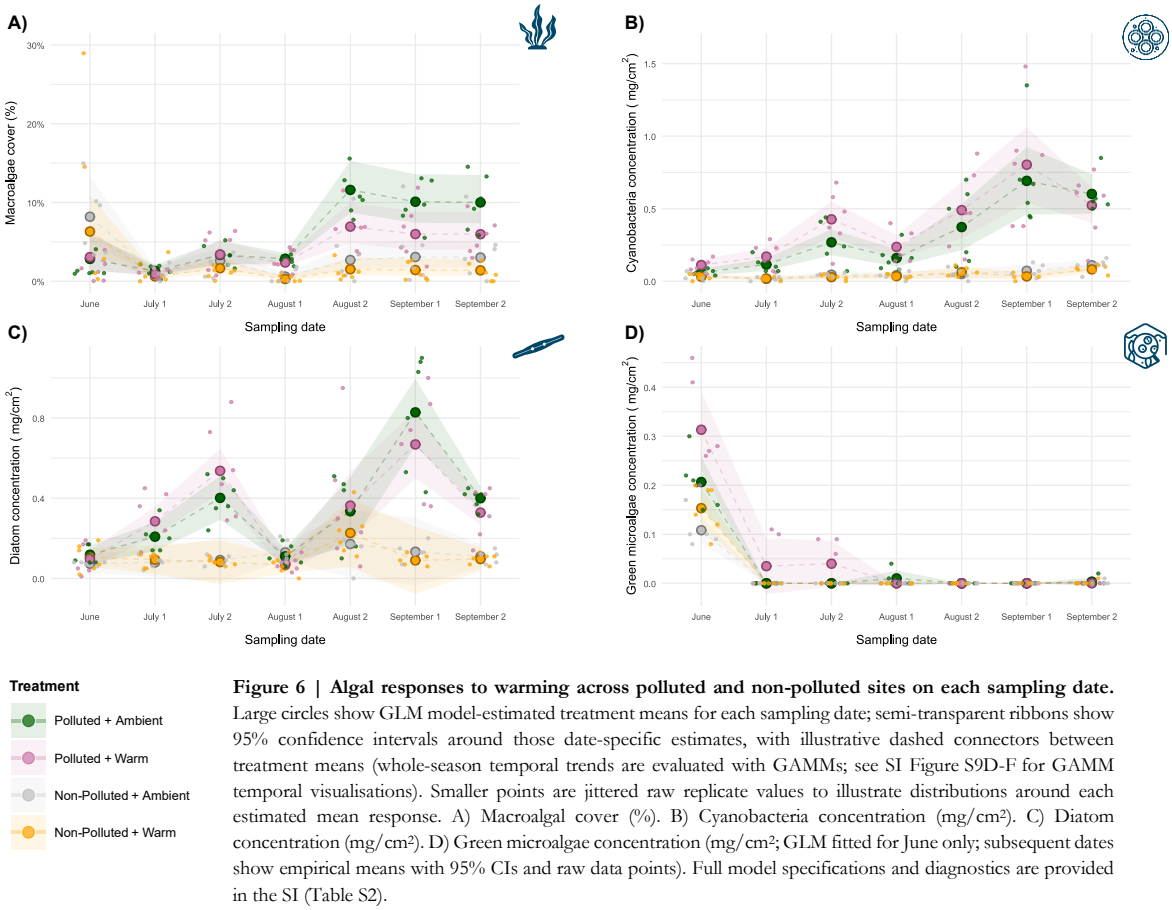


Figure 6 | Algal responses to warming across polluted and non-polluted sites on each sampling date. Large circles show GLM model-estimated treatment means for each sampling date; semi-transparent ribbons show 95% confidence intervals around those date-specific estimates, with illustrative dashed connectors between treatment means (whole-season temporal trends are evaluated with GAMMs; see SI Figure S9D-F for GAMM temporal visualisations). Smaller points are jittered raw replicate values to illustrate distributions around each estimated mean response. A) Macroalgal cover (%). B) Cyanobacteria concentration (mg/cm²). C) Diatom concentration (mg/cm²). D) Green microalgae concentration (mg/cm²; GLM fitted for June only; subsequent dates show empirical means with 95% CIs and raw data points). Full model specifications and diagnostics are provided in the SI (Table S2).

3.5 Discussion

Our study reveals complex, temporally dynamic interactions between warming and ambient sewage-associated pollution across two contrasting rocky shore sites. The prevalence of interactive responses across several response variables in our study echoes findings from several syntheses of multiple stressor studies across a variety of marine groups and life stages (Cabral et al., 2019; Gissi et al., 2021; Krishna et al., 2025; Przeslawski et al., 2015). By integrating functional-group, population, trophic, and transcriptomic responses, we demonstrate how local and global drivers can interact across ecological scales, underscoring the need to quantify interactions when informing adaptive conservation and management in dynamic coastal zones.

3.5.1 Multi-level invertebrate responses

Consistent with our predictions, the contrast between the polluted and non-polluted sites emerged as a dominant driver across several invertebrate responses at multiple levels of biological organisation. Barnacle abundance increased sharply at the polluted site throughout the season, similar to patterns reported in sewage-impacted coastal systems (Courtenay et al., 2011). This marked increase at polluted sites suggests barnacle coverage could serve as an accessible visual indicator of water quality, particularly concerning sewage pollution. Furthermore, barnacle species are particularly sensitive to increasing temperatures, suffering from desiccation due to their sessile nature (Gedan et al., 2011; Kordas & Harley, 2016; Lamb et al., 2014). Although the mean maximum temperature on black plates (38.1°C) did not exceed the thermal maximum for adult *Semibalanus balanoides* of ~42 °C (Wethey, 2002), it potentially surpassed juvenile barnacles' tolerance (Southward, 1958), perhaps contributing to mortality or settlement difficulty during recruitment. While no evidence of increased metabolic processes or antioxidant activity was detected at the molecular level, this trend likely reflects a chronic transcriptional state following prolonged exposure throughout the season, as such responses are often transient and may return to a new steady-state even when the stressor persists (López-Maury et al., 2008). GLMs and whole-season GAMMs consistently revealed positive interaction terms, with the exponentiated season-long interaction indicating a ~66% increase in barnacle abundance over the null expectation. In direct ecological terms, warming reduced barnacle abundance at both sites, but this negative

effect was weaker at the polluted site than at the non-polluted site; equivalently, the polluted-versus-non-polluted site contrast was larger under warming. Although the independent effect of site-associated pollution was large, adding warming strengthened the effect beyond the null prediction, reflecting a mild synergism at this seasonal scale. This pollution dominance is mirrored at the molecular level, as the polluted site triggered a much larger transcriptional response than warming, and further demonstrated by synergistic interactions on chaperone activity that were driven by strong pollution-associated downregulation. Similar masking has been observed in freshwater systems, where a stronger local stressor often masks regional climatic effects (Morris et al., 2022).

Barnacle body size exhibited complex temporal dynamics. In the early summer, body size was larger at the polluted site on two sampling dates but later declined below values observed at the non-polluted site (albeit statistically insignificant; see Fig. 3B). Sewage-impacted communities can show elevated secondary production and a higher proportion of smaller juveniles due to richer food supply (Cabral-Oliveira et al., 2014), consistent with elevated barnacle abundance in polluted conditions. Higher densities may also intensify competition for space, favouring smaller individuals with lower energetic costs per unit area (Marchinko et al., 2004; Senthilnathan, 2023). At the season level, the GAMM indicated that stressor main effects and their interaction were not significant, with patterns instead dominated by treatment-specific temporal trajectories. Both non-polluted treatments showed approximately linear increases through the season, whereas polluted treatments exhibited strongly non-linear trajectories, consistent with fluctuating size structure through time under sewage exposure. Mean barnacle size can reflect a composite outcome of recruitment timing, growth and density dependence, with crowding and food supply influencing size distributions and reproductive thresholds rather than producing a single monotonic response (Giménez & Jenkins, 2013; Leslie, 2005; Scrosati & Freeman, 2019; Scrosati & Holt, 2021). Moreover, our size metric (rostro-carinal plate measurements) is a morphological proxy that reflects integrated calcification, spacing of rostro-carinal plates, and growth over preceding periods; as such, it may be less sensitive to rapid changes in soft-tissue condition or short-lived stress events (Burden et al., 2014; Mondal et al., 2021), reinforcing the interpretation of GAMM patterns as reflecting cohort/growth dynamics expressed over time.

Stable isotope analyses provide further mechanistic insights. At the polluted site, barnacle tissues exhibited significantly lower $\delta^{15}N$ and $\delta^{13}C$ values, indicating incorporation of sewage-

derived nitrogen and eutrophication-enhanced carbon sources, respectively. Such effluent-based nitrogen sources can often be isotopically lighter due to rapid microbial turnover, partial denitrification/nitrification, or the labile nature of nitrogen present in effluent (Dudley and Shima, 2010; Laitano et al., 2018), then subsequently assimilated by filter-feeding barnacles. This contrasts with the more typical expectation, where anthropogenic nutrient loads elevate $\delta^{15}N$ via preferential $\delta^{14}N$ loss during microbial processing (Costanzo et al., 2005; Savage, 2005), indicating that the specific biochemical characteristics of the anthropogenic sewage effluent in our study may override conventional fractionation patterns. Likewise, a more negative $\delta^{13}C$ at the polluted site indicates a shift in carbon sourcing, typically linked to eutrophication-enhanced phytoplankton (Dudley and Shima, 2010). In contrast, warming did not alter these isotopic signatures, supporting our assumption that the warming treatment effects were localised to the settlement plates. However, warming resulted in a significantly elevated C:N ratio. This increase reflects a physiological response, potentially involving a shift towards increased allocation of carbon-rich compounds (e.g. lipids/carbohydrates) under thermal stress, while pollution did not alter this overall balance of assimilated nutrients (Zhang et al., 2018). Interestingly, our transcriptomic analyses are consistent with reduced investment in costly protein-maintenance pathways, showing selective downregulation of protein-folding genes at the polluted site, with this suppression further reinforced when warming and pollution co-occur.

The molecular responses observed here contextualise findings at higher levels of biological organisation, while revealing physiological responses following chronic exposure to warming and pollution context. Warming alone induced a relatively weak transcriptional response, dominated by the downregulation of cilium- and cytoskeleton-associated genes, potentially indicating cytoskeletal remodelling as a stress-defence mechanism (Clark et al., 2018) or energy limitation associated with impaired feeding and growth (e.g. reduced suspension-feeding efficiency) (Humphries, 2013). In contrast, the polluted-site context was associated with extensive transcriptional regulation, including upregulation of protein-turnover and DNA-repair pathways, consistent with proteotoxic and genotoxic stress typical of exposure to xenobiotics (foreign contaminants) in aquatic invertebrates inhabiting sewage-impacted environments (Freitas et al., 2023). These patterns suggest that contaminants and associated microbial by-products co-discharged with sewage, such as bacterial proliferation and their toxins, may contribute to the observed responses alongside nutrient enrichment (Albini et al., 2023), despite our field contrast being defined by a categorical site difference in

ambient sewage-associated nutrient conditions rather than a replicated pollution treatment. Consistently higher cyanobacteria concentrations at our polluted site further support the possibility that microbially derived cyanotoxins form part of this co-pollutant mixture. A clear pattern was the strong downregulation of protein-folding and chaperone genes at the polluted site, which was further intensified under combined warming. Because protein-synthesis pathways were not similarly suppressed, this may indicate a selective alteration of proteostasis. One possibility is energetic reprioritisation towards rapid growth at the expense of inducible stress-resistance pathways, a trade-off proposed for organisms under chronic stress (López-Maury et al., 2008). Alternatively, contaminant-induced interference with HSP regulation, or long-term acclimation upon chronic exposure, may contribute to dampened inducible HSP responses, as reported for intertidal crustaceans (Collins, Clark, et al., 2021; Collins, Peck, and Clark, 2021). Overall, it is likely that contaminants associated with the sewage discharge impose regulatory effects not captured by nutrient data alone, while the ecological responses we observe still reflect a realistic sewage-pollution context in which nutrient enrichment and co-occurring contaminants are tightly coupled.

The nature of the interactions observed at the molecular level differed from those observed at higher levels of biological organisation, with most classified as reversals. Such reversals are likely to arise because transcriptomic data capture responses across a wide dynamic range and large number of response variables (Brasseur et al., 2022), enabling large, sign-changing interaction effects that are more constrained in organismal or ecological traits. Gene expression can also exhibit rapid, compensatory changes that override the direction of single-stressor effects before these responses are buffered into higher-level phenotypes. Although previous multiple stressor transcriptomic studies typically report antagonisms (Brasseur et al., 2022; Delnat et al., 2020), reversals are rarely defined in molecular analyses, and many reversals detected here would have been classified as antagonistic under earlier frameworks, consistent with the existing literature. Low annotation rates prevented a detailed mechanistic interpretation, but the dominance of reversal and antagonistic interactions suggests that ambient pollution substantially reshapes thermal responses at the molecular level, partly buffering ecological impacts of warming while potentially compromising proteostasis in exposed cells.

Grazer occurrence was generally higher at the polluted site, with enrichment effects statistically supported on two of seven sampling dates. Previous work has shown mixed

gastropod responses to elevated nutrients, with abundance increasing up to a nitrate threshold before declining (Conde et al., 2020). In our study, grazers exhibited notably higher occurrence at the polluted site compared to the non-polluted site, potentially due to eutrophication supporting local primary producer proliferation as a food source (Kraufvelin et al., 2002). Elevated barnacle abundance may also have enhanced grazer settlement in polluted areas, by acting as biological facilitators and providing microhabitats, as has been observed with littorinid periwinkles (Silva et al., 2015), common in our research area. A sharp decline in grazer occurrence was observed on August 1, coinciding with high precipitation and sewage effluent release events in the area (see Supplementary Methods (Analyses); SI Fig. S10), possibly reflecting threshold-exceeding nutrients and turbidity (Cabral-Oliveira et al., 2014; Conde et al., 2020). Grazer occurrence recovered despite continued effluent discharges, perhaps due to temporary refuge or movement given motility. Additional factors such as effluent composition, unmonitored pollution events, or high footfall prior to this sampling date may have influenced this pattern. Furthermore, difficulties in model convergence owing to the high proportion of zero counts necessitated our choice of binary models (see Supplementary Methods (Experimental)), hindering ecological interpretability and nuance of findings. Moreover, at the seasonal scale, the GAMM corroborated a strong positive pollution effect on grazer occurrence, while warming and the interaction remained non-significant; temporal structure was only detectable in a subset of treatment combinations, consistent with more episodic dynamics rather than a uniform seasonal trajectory.

3.5.2 Functional-group algal responses

Algal functional groups responded strongly to nutrient pollution, with distinct patterns among macroalgae, cyanobacteria and diatoms. Experimental manipulations of nutrients and warming on rocky shores have previously demonstrated strong context dependence in algal and multi-trophic responses (e.g. O'Connor & Donohue, 2013; O'Connor et al., 2015; Mrowicki & O'Connor, 2015; White et al., 2018), and our findings align with this broader body of work. In our study, GLMs indicated macroalgal cover increased significantly at the polluted site from August 1 onward. Elevated nutrients commonly stimulate opportunistic sheet-like and filamentous macroalgae on temperate rocky shores, especially where newly available space facilitates rapid colonisation. Because macroalgal cover here was quantified on settlement plates over a single summer, this signal is most likely to reflect early-successional taxa common on our replicates such as *Ulva spp.* (e.g. *U. intestinalis, U. prolifera*),

rather than establishment of mature perennial fucoid canopies (Kraufvelin, 2007; Migné, Bordeyne & Davoult, 2025). Such successional dynamics and contrasts between opportunistic and canopy-forming taxa are well established in rocky shore ecology (Hawkins & Hartnoll, 1983; Little et al., 2009). Nutrient effects on algal cover are therefore likely to be taxon- and phenology-dependent within this system. Accordingly, our strongest inference is about how warming interacts with site context within a biologically meaningful seasonal risk window, rather than universal long-term algal regime shifts. Greater barnacle abundance at the polluted site may also have increased small-scale surface heterogeneity and propagule retention, potentially facilitating macroalgal settlement, although this interpretation remains tentative as barnacle cover was not quantified directly (Steneck et al., 2002). Whole-season GAMMs confirmed the positive influence of site-level pollution and warming's significant negative effect, consistent with thermal constraints on macroalgal physiology (Román et al., 2020). In addition to warming, solar ultraviolet radiation (UVR) exposure can stimulate enzymatic activities, increase the repair rate of photosystems and enhance photosynthesis (Ji et al., 2016; Ji & Gao, 2021), perhaps explaining initially higher coverage across all treatments. However, prolonged exposure can lead to mortality, especially when temperature thresholds are exceeded (Fernández et al., 2015; Vye et al., 2015; Zou and Gao, 2014), corroborated in our study, as near-significant warming only induced reductions in late summer. Notably, however, within this short recruitment window, the warming effect is therefore best interpreted as reduced performance or persistence of short-season recruits rather than loss of established perennial macroalgal canopies (Jackson et al., 2021; Ingólfsson & Hawkins 2008). Moreover, macroalgal abundance is tightly coupled with grazing effects of gastropods and abiotic factors (Jonsson et al., 2006; Schiel et al., 2004), which perhaps regulated excessive growth across all treatments.

Cyanobacteria concentration was consistently and significantly elevated at the polluted site from July 1 onward, while warming showed no independent effect. Interestingly, two discrete GLMs (June, July 2) detected significant positive interactions between warming and pollution context, suggesting transient, date-specific synergistic effects. In plain terms, cyanobacteria concentrations were higher than expected under the combined treatment on those dates, meaning that the polluted-versus-non-polluted site contrast became larger under warming. At the seasonal scale, the GAMM confirmed site-level pollution as the primary driver; the positive interaction was statistically significant and indicative of a mild synergism under our ±5% criterion, suggesting a modest amplification. This synergism echoes research

concluding that nutrient enrichment and warming often synergistically increase growth rate of cyanobacteria (Lürling et al., 2017; Rigosi et al., 2014); however, it is noted that this effect varies substantially among taxa (Rigosi et al., 2014). Similar context-dependent interactions between nutrient enrichment and other stressors have been reported in intertidal systems, including nutrient-by-consumer and nutrient-by-disturbance interactions (O'Connor et al., 2015; Vye et al., 2015; Vye et al., 2017). Moreover, the significant smooth terms capturing marked temporal fluctuations across treatments underscore the importance of evaluating stressor interactions across a range of temporal resolutions. Given cyanobacterial toxicity and implications for bathing water quality, these dynamics, together with evidence for cyclic shifts in biofilm composition under sewage effluent (Jaubet et al., 2024), reinforce that nutrient reduction is likely to yield the greatest mitigation of harmful blooms.

Diatoms displayed similar nutrient-driven increases, with the effect of site-level pollution significant on most dates and concentration rising through summer. This suggests nutrient pollution as the primary driver of diatom proliferation, potentially via phosphate-favoured, pollution-tolerant species, consistent with other studies (Blanco, 2024; Nunes et al., 2024; Rahman et al., 2024). This trend was notably perturbed, however, with a significant negative impact of warming on August 1. Similar patterns were observed in other algal groups, and possibly indicate that responses are subject to additional abiotic influences such as co-occurring heavy metal contamination, otherwise unaccounted for in the scope of this study. The interaction between warming and pollution was inconsistent and statistically insignificant across both discrete sampling dates and across the season. Notably however, smooth term analysis revealed that temporal trends in diatom abundance were highly significant at the polluted site, whereas no significant temporal trends were observed in non-polluted sites. This mirrors our grazer findings, whereby environmental variability associated with pollution events may have induced temporal fluctuations in concentration.

Green microalgae showed a starkly ephemeral response, with concentrations reaching near-absence following June. This contrasts strongly with other algal groups, which showed more consistent elevation at the polluted site. The June GLM nonetheless showed a positive pollution effect, consistent with eutrophication's initial boost to photosynthetic organisms (Cabral-Oliveira et al., 2014). Furthermore, with increasing and sustained thermal stress and solar radiation, concentrations showed sharp declines, aligning with the idea that moderate warming can enhance photosynthesis to a threshold, but cumulative thermal and UV stress

can abruptly override early advantages provided by both warming and pollution context (Zou and Gao, 2014).

3.5.3 Implications and future directions

Our findings emphasise the importance of temporal and multi-scale approaches for understanding multiple-stressor dynamics on rocky shores, spanning molecular to functional-group-level responses. Longer-term experiments that track adaptation and recovery under different stressor regimes are needed to separate transient from persistent responses and to inform predictive models that reflect dynamic interactions (Jackson et al., 2021; Vos et al., 2023). In our experiment, plates were installed before the first summer survey; therefore, responses observed here likely integrate not only summer conditions but also earlier treatment effects on biofilm development, settlement, early survival and subsequent seasonal dynamics (see Supplementary Methods (Experimental)). The microphytobenthos data should also be interpreted in light of the measurement approach. Because the BenthoTorch resolved diatoms, green microalgae and cyanobacteria simultaneously from the same *in situ* fluorescence reading on each plate, these outputs are not independent replicates but linked components of a shared plate-level signal. We therefore interpret them here as complementary functional-group responses within the broader multiple stressor framework, while noting that future multivariate approaches could usefully account for covariance among simultaneously derived fluorescence outputs. A combined strategy integrating laboratory experiments, transcriptomics and other 'omics' tools, computational modelling and mesocosm/field studies will be critical for developing data-driven models of how global and local stressors interact over extended periods and across levels of biological organisation. Furthermore, because passive warming was generated through plate colour, these early processes may also have been influenced by colour-associated optical cues and light environment in addition to thermal differences. Recent studies show that substrate colour can affect biofilm formation, larval recruitment, and sessile community development on marine artificial surfaces, although these effects are taxon- and context-specific and, in intertidal settings, may be weaker than those of fine-scale structural heterogeneity (Cunningham et al., 2025; Lagos et al., 2026; Schaefer et al., 2024). Accordingly, our strongest inference is to a colour-based passive warming manipulation, supported by the temperature-logging evidence and otherwise matched plate material and texture, rather than to temperature in complete isolation. Future field designs should aim to decouple thermal and optical pathways more explicitly.

Strengthening the evidence base on ecological and molecular effects can also support efforts to address sewage pollution impacts in coastal waters, improving accountability and informing actionable initiatives such as the Storm Overflows Discharge Reduction Plan in the UK, alongside stronger enforcement by regulators to prosecute ongoing offences (Department for Environment, Food, and Rural Affairs, 2023). Future studies should extend beyond nutrient differences to include co-occurring stressors such as pCO_2, silicates, heavy metals, and microbially derived toxins, providing a more complete view of variable sewage composition against a backdrop of global change. Moreover, because only one shore represented each sewage-associated site context here, broader spatial inference remains limited, and future field designs should therefore replicate contrasting site contexts where feasible, while preserving comparability in shore type, tidal height, hydrodynamics and pollution-footprint independence.

In studying stressor interactions, traditional analyses often rely on additive, linear models, where deviations indicate non-linearity (Pirotta et al., 2022; Schäfer & Piggott, 2018). However, this method oversimplifies the complexity of natural stressor-response dynamics (Schäfer et al., 2023). Statistical interactions depend not only on stressor intensities and biology, but also on the statistical process and null model employed (Duncan and Kefford, 2021; Mack et al., 2022). Accordingly, interaction classifications should be interpreted as model-based effect modification on a defined scale, and complemented with effect sizes, uncertainty, and biological context when drawing mechanistic conclusions (Schäfer et al., 2023; Spake et al., 2023).

Managing the combined effects of warming, sewage pollution, and other stressors in intertidal ecosystems is inherently complex. Stressors create distinct local footprints, yet ecosystem-level responses are shaped by context, biogeography, and spatial extent (Low et al., 2023). Experimental evidence from rocky shores demonstrates that outcomes of warming and nutrient enrichment frequently depend on consumer presence, wave exposure, and disturbance regime (O'Connor and Donohue, 2013; Mrowicki et al., 2014; Mrowicki and O'Connor, 2015; White et al., 2024). Our experiment provides a cost-effective, scalable multiple stressor approach that can be deployed more widely to test context dependence. Moreover, addressing the geographic skew in marine multiple stressor research, with a dominance of 'Global North' studies (Gissi et al., 2021) will also require fostering

collaborations and capacity with researchers in diverse regions, particularly in the 'Global South' (Dahdouh-Guebas et al., 2003; Tolochko and Vadrot, 2021), to generate geographically diverse datasets spanning different shore types, climatic regimes, land use settings, and pollution contexts for rocky shore management across spatiotemporal scales.

3.5.4 Conclusions

While experimental manipulations of warming or nutrient enrichment on rocky shores are well established, few field studies have combined experimental warming with an ambient sewage-associated site contrast, while simultaneously quantifying responses across multiple levels of biological organisation. Our study contributes to this emerging multi-level, multiple stressor field perspective. The outcomes of this work contribute towards advancing and justifying further multiple stressor research on marine and specifically intertidal ecosystems, alongside tangible management insights such as barnacle abundance as an effective visual indicator of intertidal water body health, as well as evidence of both periodic and seasonal synergisms seen in toxic cyanobacteria. This study is particularly timely in the UK, adding to the evidence base of academic knowledge supporting sanctions and stronger regulation of privatised water companies to reduce harmful sewage inputs nationwide. The feasibility of our *in situ* method should encourage informed, practical management and mitigation of both local and global stressors, with strong potential to catalyse international research and collaboration.

3.6 Supplementary information

3.6.1 Supplementary methods (experimental)

Scope of site-level pollution contrast

Because only one shore represented each pollution category, the pollution term in this experimental design is not spatially replicated. We therefore interpret it as an ambient site-context contrast between a more sewage-impacted shore (Friar's Bay) and a less impacted shore (Bastion Steps), supported by repeated nutrient verifications. This inferential limit is important in dictating warming as the experimentally replicated manipulation within each site, whereas sewage-associated pollution reflects the ambient context of the selected shores. In designing the field study, we prioritised close geographic proximity, comparable shore type, and spatially discrete site contexts to minimise broader differences in climate, exposure regime, and other local environmental conditions that would otherwise confound inferences. Increasing the number of sites would have improved nominal replication of the ambient pollution contrast, but would also have required greater spatial extent and introduced additional uncontrolled heterogeneity among shores, while making it harder to maintain independence and avoid overlap in sewage influence footprints. Practical constraints associated with permitting and maintaining comparable *in situ* installations further limited the number of feasible sites. Accordingly, site-associated pollution effects are interpreted cautiously, and repeated nutrient verification is used to support site designation rather than imply full replication of an ambient pollution treatment.

Nitrate sensor limitations and use of proportional elevation

For nitrate, we used a nitrate ion-selective electrode (ISE) on the multiparameter probe as a relative indicator of enrichment between sites, not as an absolute concentration measurement. Nitrate ISEs are susceptible to matrix interference effects in saline waters, with chloride/salinity capable of introducing substantial positive bias, and so the absolute nitrate values in Table 1 should be treated as instrument responses only, not as definitive seawater nitrate concentrations.

Because salinity was effectively the same at the polluted and non-polluted sites (36.08 vs. 36.30 PSU across the experimental period) and paired samples were taken within minutes on

each verification date, any salinity-linked bias is expected to be shared within a date, making within-date proportional differences interpretable. We therefore report and use only the proportional elevation in the nitrate-ISE signal at the polluted site relative to the non-polluted control (expressed as a ratio and plotted as % increase in Figs. 1 and S1). This enrichment signal is additionally supported by phosphate measurements from a dedicated photometric method (Table 1), which is not subject to the same nitrate-ISE chloride interference. Together, these nutrient data underpin our categorical designation of Friar's Bay as 'polluted' and Bastion Steps as 'non-polluted' for the factorial analyses.

Warming verification

Temperature loggers embedded within plates were configured to take measurements every 90 min at a 0.1 °C resolution for the duration of the study from installation, using ElectricBlue EnvLogger T2.4 loggers (27 mm hard-acrylic format; see manufacturer technical documentation: https://img1.wsimg.com/blobby/go/62cbf3ca-7d0d-4afa-9ded-6866ac65ded2/downloads/EnvLogger_documentation_package_compressed.pdf?ver=1772534277634).

Across the entire period, mean max values (i.e. maximum value recorded on each plate, averaged across treatment replicates) showed a difference of +1.6 °C (38.0 °C and 36.4 °C for black and white plates respectively). Additionally, during the summer period, when including only readings from days when low tide occurred during peak daytime hours, the mean average daily maximum (mean ADM; calculated as the residual of each plate's ADM from the grand mean on each sampling date, then averaged across treatment replicates), showed a warming increase of +0.8 °C in the warmed treatment. Additional temperature differences are shown in Table 2. While a categorical difference in warming is evident, EnvLoggers were housed in a hard and inert acrylic resin, potentially confounding the accuracy of temperature readings when embedded within an additional layer of HDPE plastic. Future iterations of the method may better capture differences in warming by using thinner plate surface layers and considering different logger encasement options, as both may have diminished the true magnitude of recorded temperature differences.

Settlement plate design and installation geometry

In many intertidal organisms, body temperature is more directly correlated with substrate as opposed to atmospheric temperatures, as the heat budget is more dominated by conduction

than convection (Denny & Harley, 2006). Warmed settlement plates, which raise body temperatures via conduction, have been employed in multiple studies (Kordas et al., 2015, 2017; Kordas & Harley, 2016; LaScala-Gruenewald & Denny, 2020), demonstrating the effectiveness of the method, particularly for organisms with high surface area in contact with substratum, such as barnacles, limpets, and prostrate algae.

Settlement plates were made of 3 cm thick black or white high-density polyethylene (HDPE) plastic squares (2 cm for treatment surface, affixed on top of an additional 1 cm white square). Each plate was 16 cm × 16 cm, topped with a centred 9 cm × 9 cm area of pale epoxy (PC-Products®; PC-11 Marine Grade Epoxy, Off White), roughly 3 mm thick. Our design was inspired by Kordas et al. (2015), with edits including expansion of surface epoxy size, logger type, and thickness of surface squares to accommodate the logger. The surfaces of plates were textured prior to epoxy application to ensure a strong bond, as it otherwise peeled off within a few months of installation. To create the heterogeneous settlement surface, we pressed a single layer of rock salt into the epoxy, which was dissolved prior to installation. The underside of the top plate was drilled using a CNC machine to create a cylindrical recess the size of the ElectricBlue EnvLogger. This allowed the EnvLogger to be sandwiched between the plates to avoid protruding hardware, which may have otherwise created additional surface heterogeneity and encouraged biased settlement.

Plates were mounted horizontally (i.e. approximately 0° relative to the local substrate), with the epoxy settlement surface facing directly upward. At both sites they were fixed to the upper faces of near-horizontal artificial substrata extending seaward from the shore. Because the biologically active settlement surface was horizontal, a compass-facing orientation in the same sense as a vertical panel was not directly applicable; instead, consistency was achieved by standardising installation height and using comparable upper horizontal surfaces across sites. The full plate assembly was approximately 3 cm thick, meaning the settlement surface stood slightly above the immediately surrounding substratum. This design is particularly suited to sessile recruits and surface-associated taxa, but responses of motile grazers should be interpreted as occupancy and use of the settlement surface rather than exhaustive abundance on the surrounding shore.

Field establishment period and interpretation

Plates were installed in January 2023 and left *in situ* until the first summer survey in June 2023 to permit natural biofilm development, settlement, and early community establishment under continuous treatment exposure. We avoid the term 'acclimatisation' here because the pre-survey interval was not a separate pre-treatment phase; rather, it formed the initial portion of the continuous experimental exposure history. Consequently, any treatment-linked differences in spring colonisation or early development are considered part of the cumulative seasonal response measured in this study, not an uncontrolled bias arising prior to the summer experiment. All plates were installed simultaneously, at the same shore height within site, and were only compared among synchronously occurring treatment groups, thereby standardising exposure history within the design. This approach is consistent with passive warming settlement-tile studies that install substrates before or at the onset of the main summer exposure period (Kordas et al., 2015, 2017; Kordas & Harley, 2016).

Automated counting

To standardise barnacle abundance counts across plates, treatments, and sampling dates, we used the CountThings mobile app workflow to analyse overhead photographs taken within the 40% stencil window to avoid edge effects (see Materials and Methods). CountThings operates via 'Counting Templates' that detect and count target objects in images, and was configured for our system using manually annotated images collected during the field-establishment period and early sampling. Training images deliberately spanned multiple barnacle morphologies, sizes (new recruits to adults), lighting conditions, epibiont cover, and epoxy textures, so that the detector would generalise across the full range of field image conditions. An additional label was used to distinguish live individuals (with an intact opercula visible) from dead individuals (opercula absent). We applied a single decision threshold across the project to balance precision and recall, and maintained quality-control measures: 1) plates with very low densities (≤10 individuals) were counted *in situ* by eye rather than by model; and 2) images showing prohibitive motion blur, glare, or water droplets were entered as NA in the dataframe and excluded. Model performance used standard metrics: precision, recall, F1 score, mean average precision (mAP), intersection-over-union (IoU), average precision per class, average recall, and false-positive rate. Detailed model architecture and internal optimisation/augmentation settings are not user-exposed as CountThings deploys templates within a proprietary environment (www.countthings.com).

RNA-seq sampling timing and interpretation

RNA-seq sampling was conducted once at the end of summer to characterise the integrated late-season transcriptional state associated with repeated warming and pollution exposure across the experimental season. It was not designed to isolate an acute minute-to-hour heat-shock response to a single low-tide event. By the time of sampling, individuals had experienced months of repeated tidal emersion cycles on their assigned plates; differential expression is therefore interpreted primarily as a late-season transcriptomic phenotype reflecting sustained exposure, acclimatory state, and/or baseline expression differences among treatment contexts. Because samples were collected during the same field session across treatments, the immediate sampling context was standardised, but, as with any single-time-point field transcriptome, acute and chronic components cannot be separated completely. We therefore interpret these RNA-seq data as an integrated end-of-season transcriptional snapshot and discuss them accordingly (López-Maury et al., 2008; Sleight et al., 2018).

3.6.2 Supplementary methods (analyses)

Grazer model convergence

Our grazer data presented statistical challenges due to the high proportion of zeros in the dataset, combined with sporadic occurrences of high counts on some sampling dates. These data characteristics led to complete separation issues, where certain predictor levels were perfectly associated with a single outcome (e.g. total grazer absence under specific conditions). In such cases, standard logistic regression struggles, as maximum likelihood estimation inflates coefficient estimates to extreme values, causing unreliable inference and misleading predicted probabilities.

We initially explored count-based formulations for grazer abundance, including Poisson, negative binomial, zero-inflated, and hurdle-type models. However, the combination of extremely sparse positive counts and very high zero frequencies led to unstable fits, poor convergence, and weak identification of separate zero-generating and count-generating processes, particularly within individual sampling dates. In addition, two-component formulations reduced ecological interpretability for this dataset, because the central biological question was whether grazers were using settlement surfaces at all, rather than precise variation in positive counts once present.

To address this, bias-reduced logistic regression (BRGLM) was used via the brglm2 package (Kosmidis & Firth, 2025). This approach applies penalty-based shrinkage to coefficient estimates, preventing overfitting and producing more accurate probability estimates. By reducing the inflation of extreme values, bias-reduced methods improve the stability and interpretability of models. This adjustment was crucial in ensuring that grazer presence probabilities were not artificially skewed due to numerical artefacts from standard logistic regression. Similarly, for the whole-season time-series analysis, we fitted a binomial logit GAMM, with stability aided by GAMM penalisation and REML estimation with select = TRUE, allowing additional shrinkage/selection of smooth terms while retaining predictions on the probability scale via the logit link.

GLM interaction conditional plots

Conditional plots provide a visual representation of how predicted response variables change under different combinations of interacting predictors. These plots are particularly useful for assessing effect modification and asymmetric responses, offering a clear visual assessment of whether stressor interactions amplify, mitigate, or shift expected outcomes (Spake et al., 2023). A fundamental advantage of conditional plots is their ability to reveal context dependence, i.e. how the effect of one predictor (e.g. warming) varies depending on the level of another predictor (e.g. pollution). In these plots, the x-axis represents one categorical stressor (here, the warming treatment), while the y-axis represents the predicted response variable (on the appropriate model scale). The two lines within each panel indicate predicted responses under different levels of the second categorical stressor (pollution), with shaded confidence bands. Panels correspond to different sampling dates and GLMs, with interaction significance provided.

GAMM model specifications

For each response variable, a generalised additive mixed model (GAMM) was fitted to capture season-long trajectories of stressor effects. These models were used because responses were sampled repeatedly across the summer and were not assumed to change linearly through time; smooth functions allow the data to determine whether temporal patterns are approximately linear or non-linear. In all GAMMs, warming treatment and pollution context (Pad_Colour and Pad_Region) were treated as fixed factors; the latter was not modelled as a random effect because each pollution context was represented by a single shore.

Time was represented as Days_Since_Start (days since the first sampling date). To allow temporal dynamics to differ among treatments, we fitted separate smooths for each warming × pollution combination using a factor-by smooth of the form (Days_Since_Start, by = interaction(Pad_Colour, Pad_Region), k = 7). The basis dimension was set to k = 7 to match the seven sampling dates, providing sufficient capacity to represent seasonal structure without pre-specifying a particular trajectory (Wood, 2025). We did not fix the smooth degrees of freedom: instead, the effective degrees of freedom (edf) for each smooth were estimated from the data under the model's smoothing penalty (i.e. we did not use the argument fx = TRUE). This allows each response variable and each treatment-specific smoothing term to retain as much or as little temporal variability as warranted, ensuring consistency across responses while avoiding arbitrary constraints or overfitting on temporal complexity. In model outputs, the edf indicates the complexity of the fitted temporal pattern: values near 1 correspond to an approximately linear trend through time, whereas larger values indicate increasing curvature. A significant smooth term indicates that the response varies with time within that treatment combination (i.e. the fitted smooth is not compatible with a flat, time-invariant effect). Notably, a smooth can be significant even when edf ≈ 1, which reflects evidence for a non-zero linear temporal trend rather than complex non-linearity.

Models were fitted by restricted maximum likelihood (REML). To account for repeated measures of the same settlement plate across sampling dates, plate identity (Pad_ID) was included as a random effect using s(Pad_ID, bs = "re"). We refer to these models as GAMMs because they include both smooth terms and a random effect, although they were fitted using mgcv::gam() rather than gamm(), with the random effect implemented as a penalised random-effect smooth. Diagnostic evaluations were conducted to assess residual normality and heteroscedasticity, ensuring model assumptions were met.

Local precipitation and effluent release events

We compared the intensity of local precipitation in Peacehaven with the duration of storm overflow sewage release events to assess whether there was an association, which may partially explain observed declines in several groups (notably grazers, barnacle size, and cyanobacteria). This was particularly relevant for observed declines in multiple group responses between July 2–August 1, which corresponded to high precipitation events and high durations of sewage effluent release events between this period.

Effluent release data were gathered from Southern Water's public repository service, 'Rivers and Seas Watch', and precipitation data were gathered from the Visual Crossing API service for the Peacehaven area. Notably, for effluent release data, we only included releases from the Newhaven Outfall (see Fig. S1). This was due to outfall monitor failures reported in other outfalls in the area, as reported in the Environment Agency Event Duration Monitoring – Storm Overflows: Annual Returns, between 2022 and at least August 2023. Therefore, while Newhaven Outfall is included here, this is a conservative representation of the true frequency or duration of effluent releases in the area.

3.6.3 Supplementary tables

Methods

Experimental

Functional group	Representative taxa (species/genus)	Common name/notes	Biotope
Barnacles (sessile)	*Semibalanus balanoides*	Acorn barnacle; dominant intertidal barnacle in experiment.	LR.FLR.Eph
	Austrominius modestus	Darwin's barnacle (invasive); present occasionally.	LR.FLR.Eph
	Chthamalus spp. (e.g. *C. montagui, C. stellatus*)	Acorn barnacles; summer recruitment in this region.	LR.HLR.MusB
Herbivorous grazers	*Patella vulgata*	Common limpet; major intertidal grazer throughout experiment.	LR.FLR.Eph
	Littorina spp. (e.g. *L. littorea, L. saxatilis, L. obtusata*)	Periwinkles; common on barnacles/within algae in experiment.	LR.FLR.Eph
	Steromphala spp. (e.g. *S. cineraria, S. umbilicalis*)	Of the family Trochidae, the top/top-shell snails; common on rocks and directly on experiment.	LR.HLR.MusB.Sem.LitX
Macroalgae (foliaceous)	*Ulva spp.* (e.g. *U. intestinalis, U. prolifera, U. lactuca*)	Sea lettuces; opportunistic green algae on nutrient-rich substrates, abundant throughout experiment.	LR.FLR.Eph
	Blidingia minima	Green fringe alga; splash/supralittoral zones.	LR.FLR.Lic.Bli
Microalgae/biofilm	Benthic diatoms (e.g. *Navicula spp., Nitzschia spp.*)	Common rock-surface diatoms (measured by BenthoTorch).	LR.FLR.Eph.EphX
	Cyanobacteria (e.g. *Oscillatoria spp., Phormidium spp.*)	Filamentous blue-green algae in biofilm (measured by BenthoTorch).	LR.LLR.F.Fves.X (collective 'biofilms')
	Green microalgae (various Chlorophyta, e.g. *Chlorella*-like genera)	Green component of biofilm (measured by BenthoTorch).	LR.LLR.F.Fves.X (collective 'biofilms')

Table S1 | Representative mid-tide genera/species known from East Sussex and southern England rocky shores, associated with each functional group. As species identity was not a focal aim of our study, these taxa illustrate the typical composition of each respective group, with details provided where common in our study region. Settlement plates at our sites were almost entirely coated by acorn barnacles (mainly *Semibalanus balanoides*). Grazers observed directly on settlement plates were exclusively herbivorous snails, chiefly common periwinkles (*Littorina spp.*) and limpets (*Patella vulgata*). Macroalgae on the plates were fast-growing green algae (sea lettuces, *Ulva spp.*) and thin algal mats. Cyanobacteria, diatoms, and green microalgae were detected via fluorometry (see Methods). Biotope column refers to the Joint Nature Conservation Committee (JNCC) UK Marine Habitat Classification (biotope) definitions, of which all listed classifications are prevalent within our sampling region and similar environments. Note that species/genera may belong to several biotopes; single predominant biotopes are provided here for clarity.

Model choices and diagnostics

Response variable	Model type	Model scale	Notes/diagnostics
Barnacle abundance	GLMs: Negative binomial GAMM: Negative binomial	Multiplicative (link = 'log')	Discrete count data, right-skewed, and overdispersed. Whole-season GAMM includes separate smooth of time per treatment, plus pad random effect to account for repeated measures.
Barnacle size	GLMs: Gaussian GAMM: Gaussian	Additive (link = 'identity')	Continuous, normally distributed on raw scale. Whole-season GAMM includes separate smooth of time per treatment, plus pad random effect to account for repeated measures.
Grazer presence	GLMs: Bias-reduced binomial logistic GAMM: Binomial logistic	Multiplicative on the odds scale (link = 'logit')	Presence/absence data with high proportion of 0s, with (quasi-)separation risk. Per-date fits use bias reduction (brglmFit) to stabilise estimates and avoid infinite/unstable coefficients. Whole-season GAMM includes separate smooth of time per treatment, plus pad random effect to account for repeated measures. The model further includes select = TRUE argument which adds shrinkage penalties to smooth terms so unsupported effects can be driven towards zero (i.e. performing smooth-term selection and stabilising the fit), as required to ensure successful convergence.
Macroalgal cover	GLMs: Beta regression GAMM: Beta regression	Multiplicative on the odds scale (link = 'logit')	Treated as proportional (bounded 0–1) with asymmetric distributions. Whole-season GAMM includes separate smooth of time per treatment, plus pad random effect to account for repeated measures.
Cyanobacteria concentration	GLMs: Tweedie GAMM: Tweedie	Additive (link = 'identity')	Continuous, non-negative, often with many 0s. Per-date GLMs fix power to default 1.5 for stability/consistency, allowing data with a point mass at zero and a continuous distribution, without adding constants. Whole-season GAMM includes separate smooth of time per treatment, plus pad random effect to account for repeated measures.
Diatom concentration	GLMs: Gaussian GAMM: Gaussian	Additive (link = 'identity')	Continuous, normally distributed on the raw scale. Whole-season GAMM includes separate smooth of time per treatment, plus pad random effect to account for repeated measures.
Green microalgae concentration	GLM (June): Gamma GAMM: NA	Additive (link = 'identity')	Continuous, non-negative, right-skewed on the raw scale. No GAMM constructed due to near-zero values across all treatments following June; therefore, no additional time points statistically modelled/analysed.

Table S2 | Model choices and diagnostics for both GLMs and GAMMs. Residuals, diagnostic plots, and model comparisons available in additional analysis R scripts.

Results

GLM model summaries

Date	Stressor	Estimate	SE	p-value	Δadd	Δobs	Exponentiated null prediction	Exponentiated observed value	Exponentiated interaction ratio	Interaction ratio 95% CI	Classification
June	Warming	−0.693	0.149	<0.001***	1.394	1.808	161.250	243.830	1.512	[1.060, 2.162]	Synergism
	Pollution	2.087	0.120	<0.001***							
	Interaction	0.414	0.182	0.023*							
July 1	Warming	−0.790	0.168	<0.001***	1.222	1.723	147.050	242.670	1.650	[1.089, 2.504]	Synergism
	Pollution	2.012	0.142	<0.001***							
	Interaction	0.501	0.212	0.018*							
July 2	Warming	−0.767	0.170	<0.001***	1.243	1.636	146.650	217.330	1.482	[0.972, 2.264]	NA
	Pollution	2.009	0.145	<0.001***							
	Interaction	0.393	0.216	0.068.							
August 1	Warming	−0.849	0.178	<0.001***	1.178	1.659	139.110	225.000	1.618	[1.038, 2.524]	Synergism (within ±5% 'additive' boundary)
	Pollution	2.026	0.152	<0.001***							
	Interaction	0.481	0.227	0.034*							
August 2	Warming	−0.961	0.177	<0.001***	1.044	1.579	124.970	213.330	1.707	[1.102, 2.651]	Synergism
	Pollution	2.005	0.148	<0.001***							
	Interaction	0.535	0.224	0.017*							
September 1	Warming	−0.963	0.183	<0.001***	1.046	1.592	124.300	214.670	1.727	[1.095, 2.729]	Synergism
	Pollution	2.009	0.155	<0.001***							
	Interaction	0.546	0.233	0.019*							
September 2	Warming	−0.980	0.181	<0.001***	1.012	1.568	123.340	215.000	1.743	[1.111, 2.741]	Synergism
	Pollution	1.992	0.153	<0.001***							
	Interaction	0.556	0.230	0.016*							

Table S3 | Barnacle abundance GLMs (log scale).

Date	Stressor	Estimate	SE	p-value	Δadd	Δobs	Null prediction	Observed value	±5% band	Interaction 95% CI	Classification
June	Warming	−0.054	0.167	0.752	-0.05	0.171	2.763	2.984	±0.138	[−0.243, 0.685]	NA
	Pollution	0.003	0.167	0.984							
	Interaction	0.221	0.237	0.361							
July 1	Warming	−0.126	0.140	0.376	0.236	0.445	3.043	3.252	±0.152	[−0.178, 0.597]	NA
	Pollution	0.362	0.140	0.017*							
	Interaction	0.209	0.198	0.302							
July 2	Warming	−0.096	0.154	0.540	0.318	0.169	3.248	3.100	±0.162	[−0.575, 0.278]	NA
	Pollution	0.414	0.154	0.014*							
	Interaction	−0.148	0.218	0.504							
August 1	Warming	−0.232	0.155	0.149	-0.52	-0.295	2.585	2.810	±0.129	[−0.204, 0.654]	NA
	Pollution	−0.288	0.155	0.078.							
	Interaction	0.225	0.219	0.316							
August 2	Warming	−0.300	0.176	0.105	-0.591	-0.280	2.652	2.964	±0.133	[−0.177, 0.800]	NA
	Pollution	−0.292	0.176	0.114							
	Interaction	0.312	0.249	0.226							
September 1	Warming	−0.229	0.169	0.188	-0.578	-0.205	2.550	2.923	±0.127	[−0.094, 0.840]	NA
	Pollution	−0.349	0.169	0.052.							
	Interaction	0.373	0.238	0.133							
September 2	Warming	−0.238	0.223	0.300	-0.431	-0.246	2.911	3.096	±0.146	[−0.435, 0.804]	NA
	Pollution	1.992	0.153	<0.001***							
	Interaction	0.556	0.230	0.016*							

Table S4 | Barnacle size GLMs (Gaussian, identity scale).

Date	Stressor	Estimate	SE	p-value	Δadd	Δobs	Null probability	Observed probability	Interaction odds ratio	Interaction ratio 95% CI	Classification
June	Warming	0.000	2.242	1.000	3.864	3.864	0.786	0.786	1.000	[0.006, 179.037]	NA
	Pollution	3.864	1.872	0.039*							
	Interaction	0.000	2.647	1.000							
July 1	Warming	0.000	2.242	1.000	3.153	5.13	0.643	0.929	7.222	[0.026, 2021.585]	NA
	Pollution	3.153	1.800	0.080.							
	Interaction	1.977	2.875	0.492							
July 2	Warming	0.000	2.242	1.000	3.864	3.153	0.786	0.643	0.491	[0.003, 79.632]	NA
	Pollution	3.864	1.872	0.039*							
	Interaction	−0.712	2.596	0.784							
August 1	Warming	−1.977	1.800	0.272	-3.954	-1.977	0.011	0.071	7.222	[0.026, 2021.585]	NA
	Pollution	−1.977	1.800	0.272							
	Interaction	1.977	2.875	0.492							
August 2	Warming	−1.266	1.872	0.499	1.333	2.599	0.508	0.786	3.545	[0.036, 348.932]	NA
	Pollution	2.599	1.407	0.065.							
	Interaction	1.266	2.342	0.589							
September 1	Warming	0.000	1.407	1.000	1.299	3.864	0.500	0.929	13.000	[0.152, 1115.238]	NA
	Pollution	1.299	1.287	0.313							
	Interaction	2.565	2.271	0.259							
September 2	Warming	−1.977	1.800	0.272	1.176	3.153	0.643	0.929	7.222	[0.026, 2021.585]	NA
	Pollution	3.153	1.800	0.080.							
	Interaction	1.977	2.875	0.492							

Table S5 | Grazer presence probability GLMs (logit scale).

Date	Stressor	Estimate	SE	p-value	Δadd	Δobs	Null proportion	Observed proportion	Odds ratio	Interaction ratio 95% CI	Classification
June	Warming	−0.280	0.399	0.483	-1.398	-1.037	0.022	0.031	1.435	[0.409, 5.032]	NA
	Pollution	−1.118	0.456	0.014*							
	Interaction	0.361	0.640	0.573							
July 1	Warming	−0.520	0.410	0.204	-0.286	-0.129	0.008	0.009	1.170	[0.399, 3.428]	NA
	Pollution	0.234	0.358	0.513							
	Interaction	0.157	0.549	0.775							
July 2	Warming	−0.460	0.386	0.233	-0.204	0.273	0.021	0.034	1.611	[0.603, 4.303]	NA
	Pollution	0.256	0.338	0.449							
	Interaction	0.476	0.502	0.342							
August 1	Warming	−0.754	0.392	0.055.	0.843	1.406	0.014	0.024	1.757	[0.757, 4.080]	NA
	Pollution	1.596	0.270	<0.001***							
	Interaction	0.564	0.430	0.190							
August 2	Warming	−0.582	0.438	0.185	0.974	0.991	0.068	0.069	1.017	[0.377, 2.746]	NA
	Pollution	1.555	0.332	<0.001***							
	Interaction	0.017	0.507	0.974							
September 1	Warming	−0.788	0.436	0.071.	0.475	0.696	0.049	0.060	1.248	[0.458, 3.401]	NA
	Pollution	1.263	0.323	<0.001***							
	Interaction	0.221	0.512	0.666							
September 2	Warming	−0.795	0.439	0.070.	0.479	0.714	0.048	0.060	1.265	[0.462, 3.463]	NA
	Pollution	1.274	0.325	<0.001***							
	Interaction	0.235	0.514	0.648							

Table S6 | Macroalgal cover GLMs (logit scale).

Date	Stressor	Estimate	SE	p-value	Δadd	Δobs	Null prediction	Observed value	Interaction 95% CI	±5% band	Classification
June	Warming	−0.005	0.012	0.677	0.018	0.075	0.055	0.112	[0.006, 0.114]	±0.003	Synergism
	Pollution	0.023	0.016	0.148							
	Interaction	0.057	0.027	0.047*							
July 1	Warming	0.002	0.008	0.832	0.100	0.153	0.117	0.170	[−0.021, 0.135]	±0.006	NA
	Pollution	0.098	0.023	<0.001***							
	Interaction	0.053	0.038	0.180							
July 2	Warming	−0.017	0.015	0.264	0.207	0.382	0.252	0.427	[0.022, 0.343]	±0.013	Synergism
	Pollution	0.223	0.047	<0.001***							
	Interaction	0.175	0.080	0.040*							
August 1	Warming	−0.007	0.015	0.657	0.112	0.195	0.153	0.237	[−0.020, 0.195]	±0.008	NA
	Pollution	0.118	0.033	0.002**							
	Interaction	0.083	0.053	0.132							
August 2	Warming	0.012	0.028	0.676	0.335	0.440	0.385	0.490	[−0.155, 0.382]	±0.019	NA
	Pollution	0.323	0.083	<0.001***							
	Interaction	0.105	0.131	0.431							
September 1	Warming	−0.038	0.025	0.138	0.582	0.732	0.653	0.803	[−0.207, 0.519]	±0.033	NA
	Pollution	0.620	0.120	<0.001***							
	Interaction	0.150	0.179	0.413							
September 2	Warming	−0.028	0.025	0.271	0.463	0.413	0.573	0.523	[−0.245, 0.142]	±0.029	NA
	Pollution	0.492	0.073	<0.001***							
	Interaction	−0.050	0.097	0.613							

Table S7 | Cyanobacteria concentration GLMs (Tweedie, identity scale).

Date	Stressor	Estimate	SE	p-value	Δadd	Δobs	Null prediction	Observed value	Interaction 95% CI	±5% band	Classification
June	Warming	0.032	0.032	0.327	0.077	0.022	0.150	0.095	[−0.142, 0.032]	±0.008	NA
	Pollution	0.045	0.032	0.169							
	Interaction	−0.055	0.045	0.231							
July 1	Warming	0.013	0.049	0.788	0.142	0.205	0.222	0.285	[−0.073, 0.199]	±0.011	NA
	Pollution	0.128	0.049	0.017*							
	Interaction	0.063	0.069	0.372							
July 2	Warming	−0.010	0.074	0.894	0.300	0.445	0.392	0.537	[−0.061, 0.351]	±0.020	NA
	Pollution	0.310	0.074	<0.001***							
	Interaction	0.145	0.105	0.183							
August 1	Warming	−0.063	0.028	0.033*	−0.083	-0.057	0.047	0.073	[−0.050, 0.103]	±0.002	NA
	Pollution	−0.020	0.028	0.479							
	Interaction	0.027	0.039	0.504							
August 2	Warming	0.055	0.115	0.637	0.218	0.192	0.390	0.363	[−0.345, 0.291]	±0.020	NA
	Pollution	0.163	0.115	0.170							
	Interaction	−0.027	0.162	0.871							
September 1	Warming	−0.043	0.114	0.708	0.652	0.535	0.785	0.668	[−0.432, 0.199]	±0.039	NA
	Pollution	0.695	0.114	<0.001***							
	Interaction	−0.117	0.161	0.477							
September 2	Warming	−0.013	0.041	0.747	0.277	0.218	0.387	0.328	[−0.172, 0.055]	±0.019	NA
	Pollution	0.290	0.041	<0.001***							
	Interaction	−0.058	0.058	0.324							

Table S8 | Diatom concentration GLMs (Gaussian, identity scale).

Date	Stressor	Estimate	SE	p-value	Δadd	Δobs	Null prediction	Observed value	Interaction ratio 95% CI	±5% band	Classification
June	Warming	0.045	0.023	0.062.	0.143	0.205	0.252	0.313	[−0.036, 0.168]	±0.013	NA
	Pollution	0.098	0.028	0.002**							
	Interaction	0.062	0.051	0.240							

Table S9 | Green microalgae concentration GLM (June only: Gamma, identity scale).

GAMM model summaries

Stressor	Estimate	SE	p-value	Δadd	Δobs	Exponentiated null prediction	Exponentiated observed value	Exponentiated interaction ratio	Interaction ratio 95% CI	Classification
Warming	−0.887	0.214	<0.001***	1.200	1.708	132.950	220.780	1.661	[0.924, 2.984]	Synergism (marginal significance; within ±5% 'additive' boundary)
Pollution	2.087	0.210	<0.001***							
Interaction	0.507	0.299	0.0897.							

Smooth term	edf	df	χ^2	p-value
Days since start (Ambient, non-polluted)	1.000	1.000	1.437	0.231
Days since start (Warm, non-polluted)	1.000	1.000	3.913	0.048*
Days since start (Ambient, polluted)	1.000	1.000	0.674	0.412
Days since start (Warm, polluted)	1.802	2.236	22.352	<0.001

Table S10 | Barnacle abundance GAMM (log scale).

Stressor	Estimate	SE	p-value	Δadd	Δobs	Null prediction	Observed value	Interaction 95% CI	±5% band	Classification
Warming	−0.182	0.134	0.177	−0.231	-0.034	2.822	3.019	[−0.176, 0.569]	±0.141	NA
Pollution	−0.049	0.134	0.716							
Interaction	0.197	0.190	0.302							

Smooth term	edf	df	F-statistic	p-value
Days since start (Ambient, non-polluted)	1.000	1.000	34.551	<0.001***
Days since start (Warm, non-polluted)	1.000	1.000	13.377	<0.001***
Days since start (Ambient, polluted)	5.186	5.747	6.434	<0.001***
Days since start (Warm, polluted)	3.965	4.738	2.435	0.031*

Table S11 | Barnacle size GAMM (Gaussian, identity scale).

Stressor	Estimate	SE	p-value	Δadd	Δobs	Null probability	Observed probability	Odds ratio	Interaction ratio 95% CI	Classification
Warming	−1.640	1.225	0.181	1.225	4.962	0.294	0.950	41.984	[0.259, 6811.937]	NA
Pollution	2.865	0.768	<0.001*							
Interaction	3.737	2.597	0.150							

Smooth term	edf	df	χ^2	p-value
Days since start (Ambient, non-polluted)	0.790	6.000	3.083	0.050*
Days since start (Warm, non-polluted)	0.147	6.000	0.161	0.317
Days since start (Ambient, polluted)	1.707	6.000	4.115	0.079.
Days since start (Warm, polluted)	3.517	6.000	9.629	0.024*

Table S12 | Grazer presence probability GAMM (logit scale).

Stressor	Estimate	SE	p-value	Δadd	Δobs	Null proportion	Observed proportion	Odds ratio	Interaction ratio 95% CI	Classification
Warming	−0.608	0.297	0.041*	0.024	0.341	0.026	0.035	1.373	[0.615, 3.064]	NA
Pollution	0.632	0.285	0.027*							
Interaction	0.317	0.410	0.439							

Smooth term	edf	df	χ^2	p-value
Days since start (Ambient, non-polluted)	4.102	4.845	37.770	<0.001***
Days since start (Warm, non-polluted)	3.644	4.376	74.220	<0.001***
Days since start (Ambient, polluted)	3.869	4.622	91.930	<0.001***
Days since start (Warm, polluted)	2.451	3.031	37.080	<0.001***

Table S13 | Macroalgal cover GAMM (logit scale).

Stressor	Estimate	SE	p-value	Δadd	Δobs	Null prediction	Observed value	Interaction 95% CI	±5% band	Classification
Warming	−0.011	0.009	0.188	0.257	0.343	0.309	0.395	[0.009, 0.162]	±0.016	Synergism (within ±5% 'additive' boundary)
Pollution	0.268	0.026	<0.001***							
Interaction	0.086	0.039	0.030*							

Smooth term	edf	df	F-statistic	p-value
Days since start (Ambient, non-polluted)	1.906	2.365	4.347	0.011*
Days since start (Warm, non-polluted)	1.531	1.880	3.742	0.044*
Days since start (Ambient, polluted)	2.019	2.479	33.643	<0.001***
Days since start (Warm, polluted)	1.000	1.000	64.495	<0.001***

Table S14 | Cyanobacteria concentration GAMM (Tweedie, identity scale).

Stressor	Estimate	SE	p-value	Δadd	Δobs	Null prediction	Observed value	Interaction 95% CI	±5% band	Classification
Warming	−0.004	0.047	0.927	0.226	0.223	0.339	0.336	[−0.133, 0.127]	±0.017	NA
Pollution	0.230	0.047	<0.001***							
Interaction	−0.003	0.066	0.963							

Smooth term	edf	df	F-statistic	p-value
Days since start (Ambient, non-polluted)	1.000	1.000	1.638	0.203
Days since start (Warm, non-polluted)	1.000	1.000	0.250	0.618
Days since start (Ambient, polluted)	5.777	5.979	31.358	<0.001***
Days since start (Warm, polluted)	5.818	5.986	23.559	<0.001***

Table S15 | Diatom concentration GAMM (Gaussian, identity scale).

Stable isotope analysis (SIA) summaries

Treatment	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	Mean C:N	SD C:N
Non-polluted + Ambient	11.705	0.288	−17.235	0.221	4.107	0.083
Non-polluted + Warm	11.629	0.338	−17.256	0.604	4.227	0.136
Polluted + Ambient	11.287	0.320	−18.404	0.155	4.134	0.099
Polluted + Warm	11.371	0.275	−18.343	0.166	4.210	0.079
Alanine (standard)	−1.479	0.057	−27.153	0.066	2.585	0.034
IAEA-CH-6 (standard)	−4.614	1.619	−10.540	0.245	290.366	173.670
Seal collagen (standard)	16.031	0.073	−12.942	0.126	2.759	0.053

Table S16 | SIA summary statistics.

Isotope	Stressor	Sum of squares	Mean squares	F-value	p-value
$\delta^{15}N$	Pollution	0.628	0.628	6.814	0.018*
	Warming	0.000	0.000	0.001	0.975
	Interaction	0.035	0.035	0.379	0.546
	Residuals	1.659	0.092	NA	NA
$\delta^{13}C$	Pollution	6.984	6.984	64.899	2.22e-07*
	Warming	0.002	0.002	0.020	0.890
	Interaction	0.009	0.009	0.086	0.772
	Residuals	1.937	0.108	NA	NA
C:N ratio	Pollution	0.001	0.001	0.108	0.746
	Warming	0.053	0.053	5.330	0.033*
	Interaction	0.003	0.003	0.267	0.612
	Residuals	0.179	0.010	NA	NA

Table S17 | SIA ANOVAs.

3.6.4 Supplementary figures

Methods

Experimental verifications

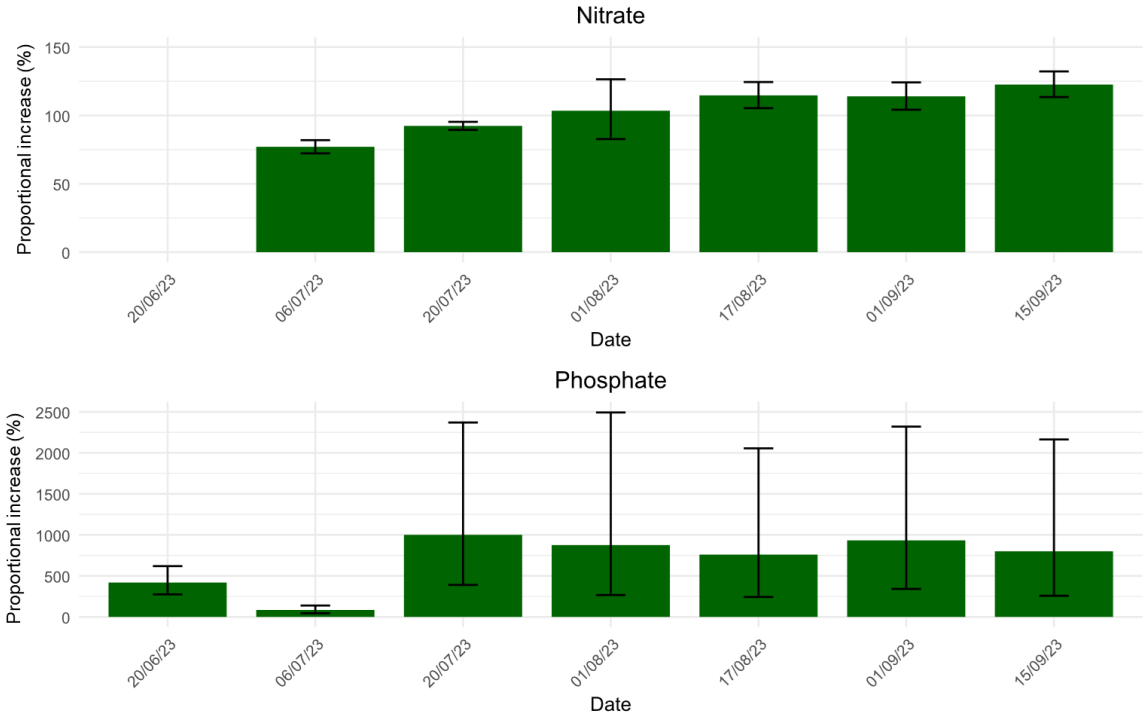


Figure S1: Proportional elevation in nitrate and phosphate at the polluted site relative to the non-polluted site throughout the experimental period. For each sampling date and nutrient, five water samples were collected from each site and averaged. Bars show the estimated percentage increase in mean concentration at the polluted site, calculated as $100 \times (R - 1)$, where R is the ratio of polluted to non-polluted mean concentrations on the natural-log scale. Error bars denote 95% confidence intervals derived using the log-ratio delta method from the standard errors of the mean concentrations in each site. Nitrate measurements for 20/06/2023 were omitted due to probe failure.

Results

GLM conditional plots

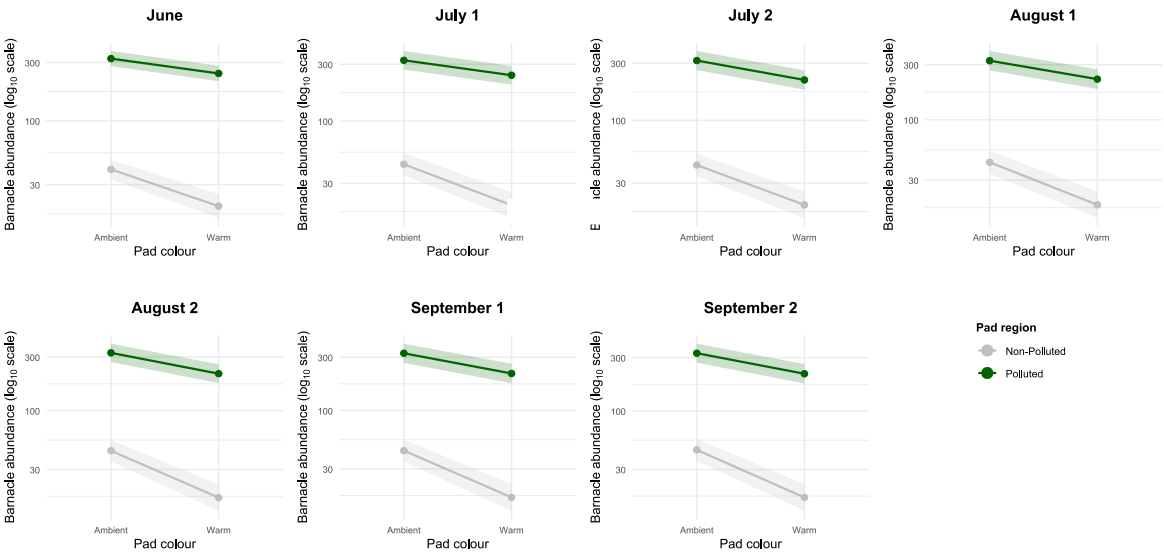


Figure S2 | Barnacle abundance GLM conditional plots.

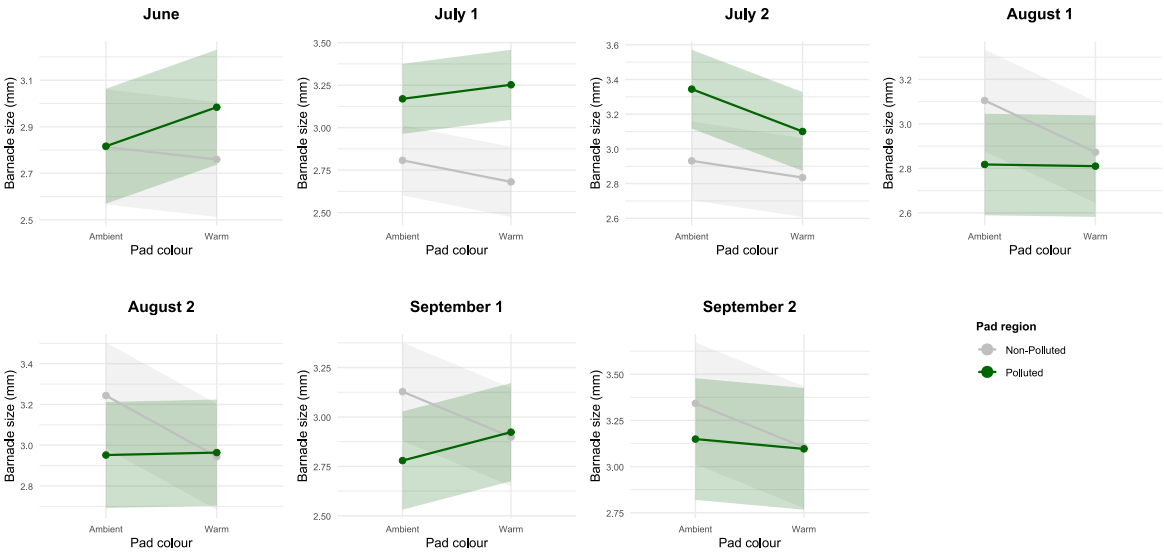


Figure S3 | Barnacle size GLM conditional plots.

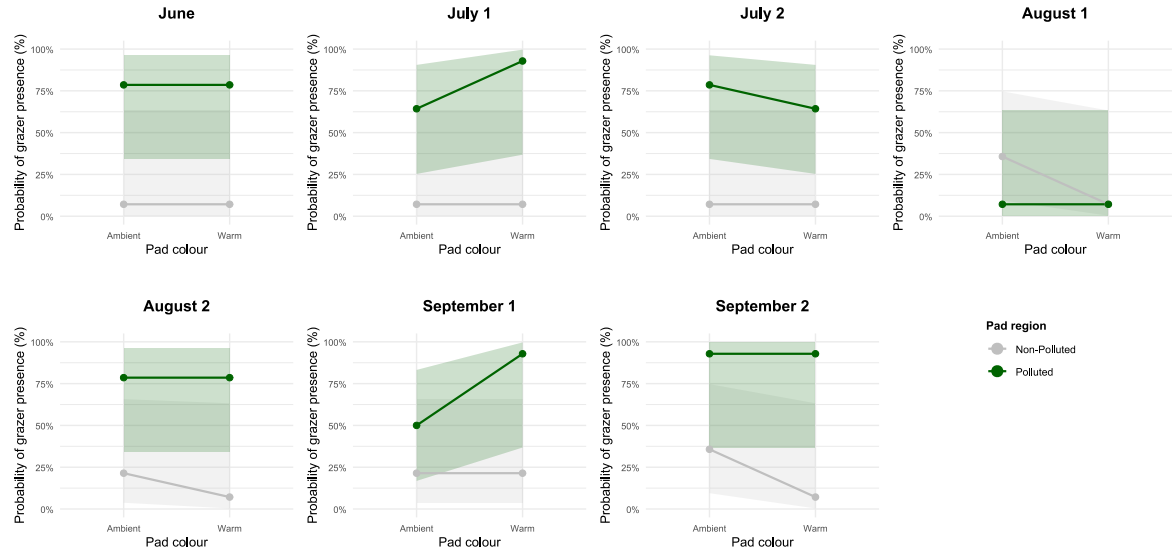


Figure S4 | Grazer presence probability GLM conditional plots.

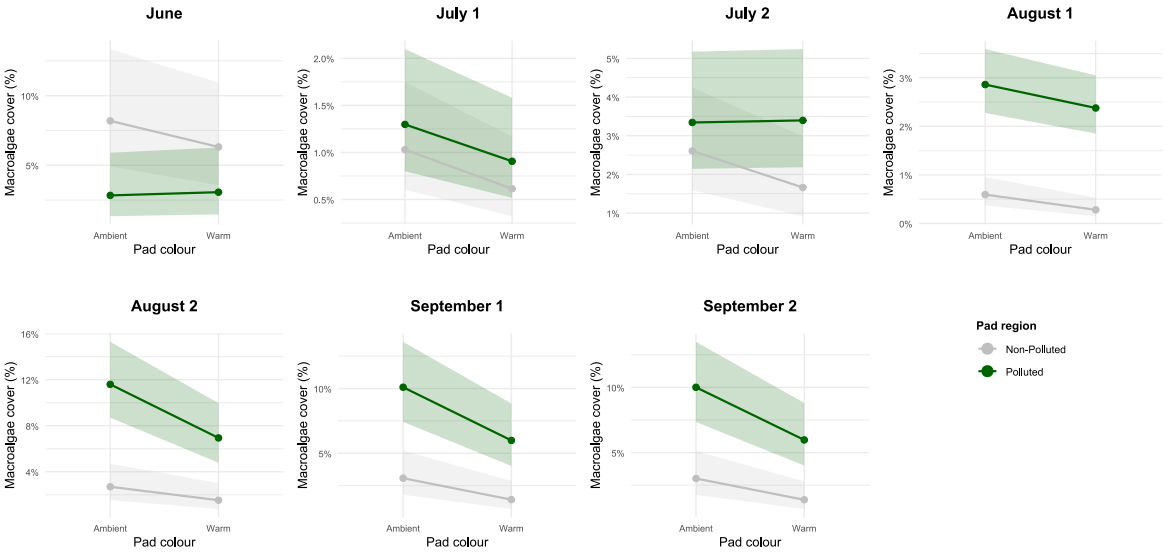


Figure S5 | Macroalgal cover GLM conditional plots.

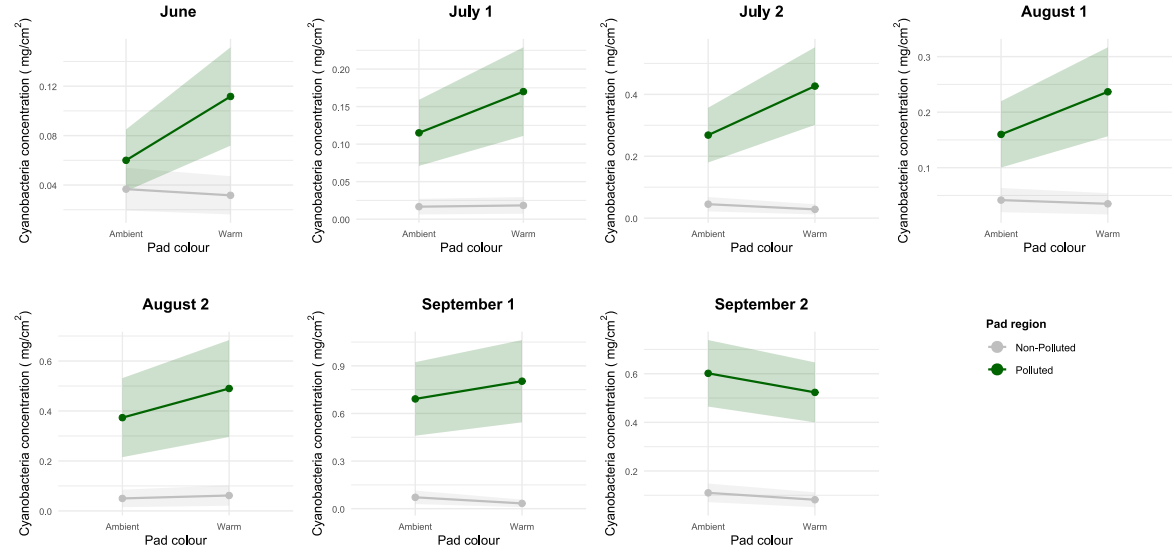


Figure S6 | Cyanobacteria concentration GLM conditional plots.

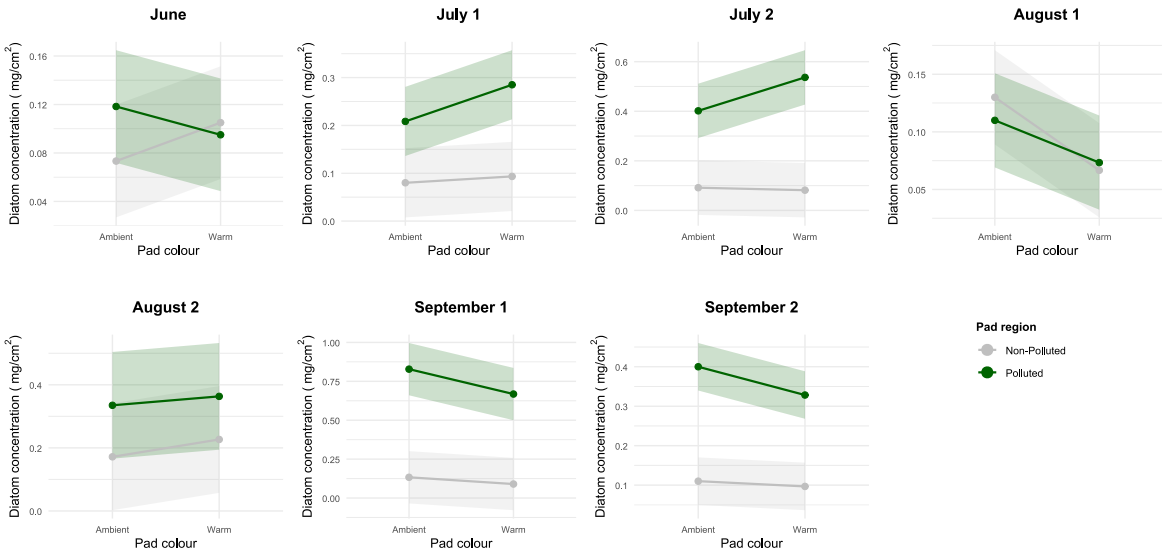


Figure S7 | Diatom concentration GLM conditional plots.

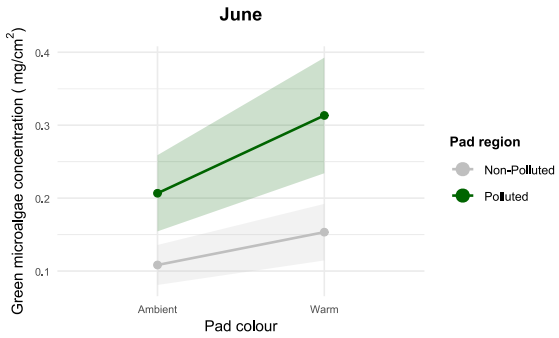


Figure S8 | Green microalgae concentration GLM conditional plot (June only).

GAMM model summaries

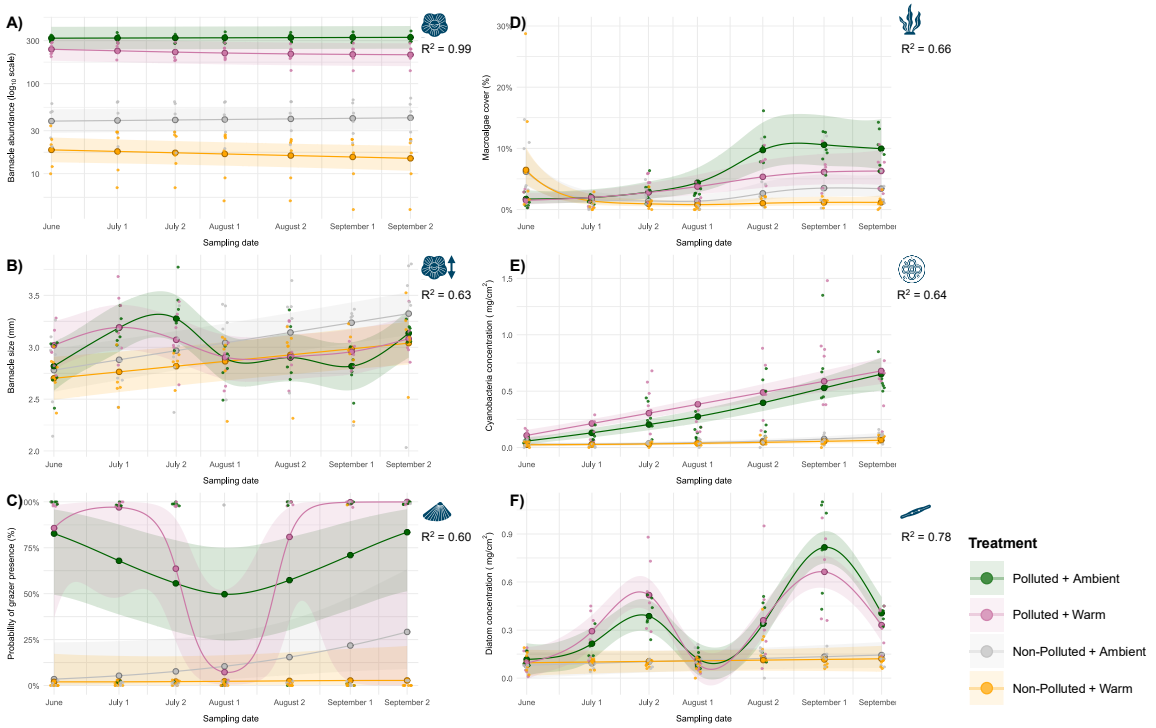


Figure S9: Responses over time to warming and nutrient pollution from generalised additive models (GAMMs). Fitted GAMM curves are plotted against days since the start of summer linking large circles representing model-estimated means per sampling date, where a smooth term captures potential non-linear temporal trends across stressor combinations throughout the summer season (see 'GAMM model summaries' and SI Table S2 for model details). Shaded ribbons represent 95% CIs, and surrounding individual points are jittered raw data for each replicate to illustrate distributions. The adjusted R^2 values indicate model fit. A) Barnacle abundance; B) Barnacle size; C) Grazer presence; D) Macroalgal cover; E) Cyanobacteria concentration; F) Diatom concentration.

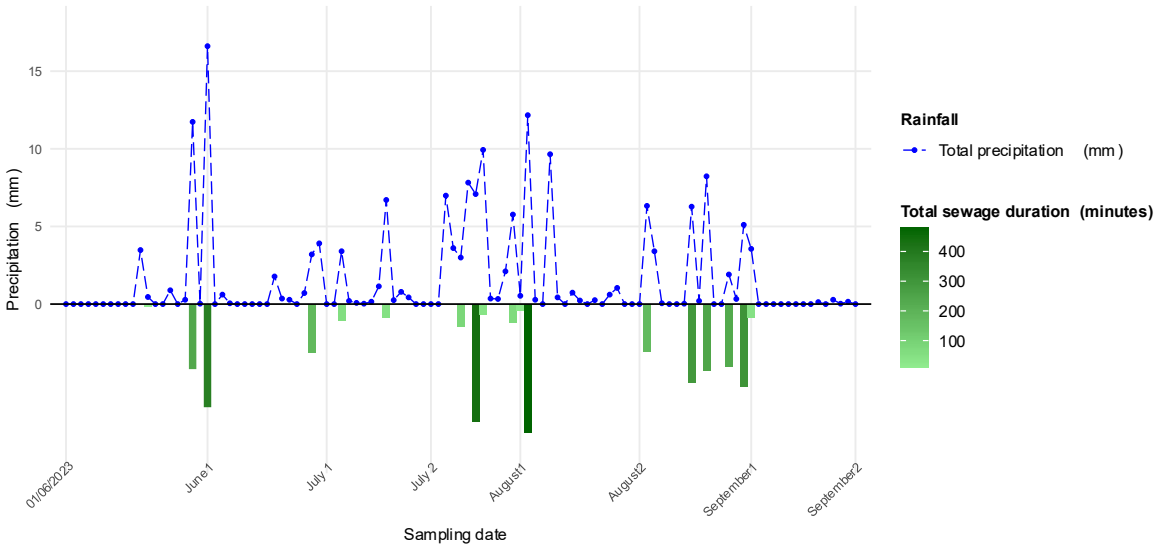


Figure S10 | Comparison of precipitation and sewage release events. Precipitation data for Peacehaven sourced from the Visual Crossing database, showing daily precipitation (mm). Heat-mapped bars indicate the total daily duration of sewage release events at Newhaven Outfall (see Figure S1), with duration (minutes) indicated by colour and length of bars. Figure shows from June 1st 2023, prior to the June 1 sampling date (June 20th) for additional context.

3.7 Supplementary document: Plate construction

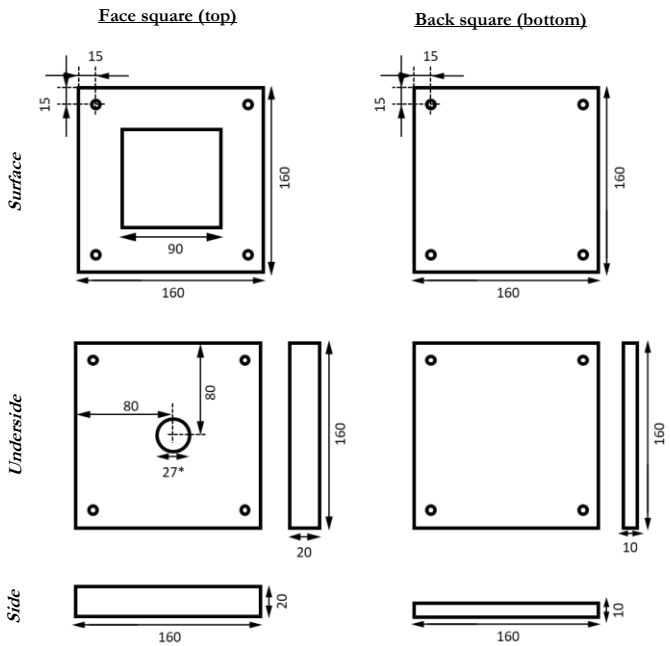
These building instructions are to be used as a guide. Availability of materials will vary, but are permissible provided the dimensions, colour difference, and sizes of materials are the same. Example suppliers have been provided throughout, but if the same piece cannot be sourced, ensure the specifications and quality are matched.

3.7.1 Plate specifications

Values given are in millimetres (mm). Visual dimensions not to scale. Note, measurements with an asterisk '*' are customisable to accommodate the dimension of the logger subsequently embedded.

HDPE plastic squares should be sourced following the below specifications:

- Face (top) squares: 160 mm × 160 mm × 20 mm: 12 black, and 12 white (following experimental method employed in this paper).
- Back (bottom) squares: 160 mm × 160 mm × 10 mm: 24 (following experimental method; colour does not matter, and the number must match the total number of face squares).
- Suggested UK provider: Bay Plastics: https://www.plasticstockist.com/HDPE-Sheet-PE300.aspx.



3.7.2 Logger installation

The temperature logger will be placed into the underside of the face plate, sandwiched between the face and back plates.

- Suggested temperature loggers: EnvLogger T2.4 (27 mm): https://electricblue.eu/temperature-envloggers.

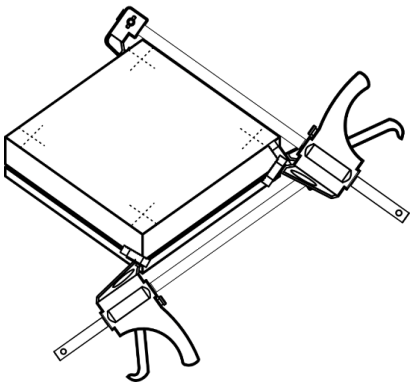
Create a niche for the temperature logger to sit in the centre of the face plate, so that it lies flat. To do so, there are two options:

1. Manually drill the circular niche into the underside of the face square, using an appropriately sized flat drill bit (e.g. a 27 mm flat drill bit for a temperature logger of 27 mm diameter as employed in this study).
    - Must ensure that the depth of the recession is only as deep as needed to accommodate the logger (e.g. 11 mm depth for loggers used in this study); drilling deeper risks going through the plate, and will not ensure the logger is flush.

2. Use a CNC machine to consistently and accurately drill the recession with the exact measurements to accommodate the logger.
    - This method was employed in this study, by outsourcing to the same retailer that provided the HDPE plastic at an additional fee (Bay Plastics).
    - This method is preferable for consistency and logistical ease, however, poses more financial cost.

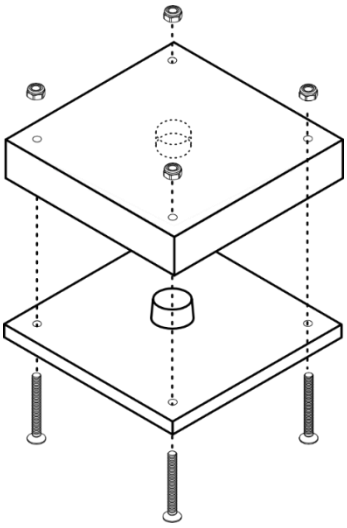
Next, we then clamp the face and back plate together; this will ensure they are aligned to create holes to drill and secure them together, with the logger then sandwiched between.

1. The bolt holes need to be created to attach the face plate to the back plate.



- Clamp the plates together using at least two quick clamps, or g-clamps.
- Measure approximately 15 mm both ways from each corner of the plate, and draw lines 90° from the edges until they cross.
- Using a 6 mm drill bit, drill through both plates fully.
    - If using a hand drill, there is likely to be slight variation between each hole drilled; the face and back squares should always align with the correct drill holes. Etching a pattern/number into one of the sides of both the face, and the back plates is recommended, to ensure consistent square pairs and orientation.
    - *Tip: slide an M6 bolt into the holes as they are drilled to prevent sliding.*

2. Embed the temperature logger.



- Ensure that the logger is set up to the recording/logging parameters you desire, and is logging correctly (depending on the recording range of the logger, you can calibrate either before, or after installation; ensure you check this prior).
- Place the logger in the niche in the underside of the face square, with the sensor against the top of the face plate.
- Insert M6 50 mm bolts into the predrilled holes from the back of the back square, through to the face square, so that the M6 bolts can be tightened on the face plate side using a spanner (this is to ensure that the back plate can lie flat on the installation surface, without protrusion from bolts).
    - Suggested bolts: M6 Hexagon Nylon Locking Nuts.: https://www.accu.co.uk/hexagon-nylon-locking-nuts/7948-HNN-M6-A2.
    - Suggested screws: M6 × 50mm Socket Countersunk Screws.: https://www.accu.co.uk/countersunk-socket-head-screws/5492-SSK-M6-50-A2.

3.7.3 Epoxy surface application

Now you will need to attach an epoxy surface to the front plate. This is the actual experimental, colonisation region, which will be texturised in order to simulate natural substrate.

1. Mark out the area using masking/painter's tape.
   - 9 cm × 9 cm in the centre (following the area employed in this study).

2. Texturise/roughen the 9 cm square in order to ensure the epoxy will adequately stick, and not peel off (this is a very likely possibility if not texturised).
   - Can cross hatch texturise using a blade/scalpel, or a sanding hand tool (e.g. Dremel rotary multitool).

3. Mix the epoxy and apply onto the square within the area of the masking tape border, ensuring layer is not too thick (no more than ~5mm; the thicker, the more likely to peel off).
   - Apply quickly, depending on the cure time.
   - Suggested brand: PC-Products 080115 PC-11 Marine Grade Paste Epoxy: https://pcepoxy.co.uk/products/pc-11-paste-epoxy.

4. Apply rock salt and push into the surface of the wet epoxy; this will create the bumpy texture for settlement.

5. Before the epoxy dries completely, remove the tape.

6. When the epoxy has completely cured, rinse the surface of the plates with boiling water thoroughly to remove the rock salt.

7. With your completed plate, drill a hole on the left and right of the epoxy square; this is where the screw will go through to attach onto the substrate (recommended size, 8mm diameter hole).

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4

Research Article

Chapter 4 | Global Intertidal Community Responses to Warming and Nutrient Enrichment

4.0 Commentary and statement of authorship

Chapter 4 extends the thesis from a temporally resolved local case study, to a coordinated multi-site experiment, designed to test how and why multiple stressor outcomes vary across biogeographic contexts. It retains the same core passive warming settlement plate methodology used in Chapter 3, ensuring continuity in the physical substrate manipulation. The inferential focus shifts from within-site seasonal dynamics to cross-site context dependence. The design also expands the causal framing beyond direct stressor–response pathways by explicitly evaluating how effects propagate through communities via biotic linkages among functional groups. The resulting experiment spans 11 international locations across 22 paired sites (11 nutrient-enriched and 11 non-enriched) with factorial manipulation of substrate warming and local nutrient enrichment, and functional-group responses measured under standardised protocols. This study represents a notably broad spatial extent

of distributed field experiments; a first-of-its-kind for multiple stressor experiments at the land–sea interface.

The study was practically implemented via a broad collaborator network recruited through social media, comprising over 30 researchers across 19 institutions and five continents, responsible for deployment and sampling. This approach aligns with wider critiques of 'parachute science' in field-based research by ensuring equitable acknowledgement of collaborator contributions, and further demonstrates the importance of embedding local expertise in study execution and interpretation when inference spans diverse jurisdictions and socioecological contexts (Stefanoudis et al., 2021).

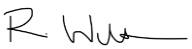
This chapter is further motivated by documented limits of geographically narrow evidence, which remains biased towards the Northern Hemisphere in multiple stressor ecology (Gissi et al., 2021; Thyrring et al., 2025). The experiment therefore tests whether independent and interactive stressor effects observed at the site-level generalise to the global mean and moves beyond abstract attribution of 'context dependence' by quantifying potential drivers of heterogeneity across sites. The chapter employs meta-regressions and biogeographic analyses to evaluate environmental moderators of stressor sensitivity at the site-level and applies structural equation modelling to test whether effects on focal taxa are direct or mediated through changes in other ecological groups.

Chapter 4 consolidates the thesis' central argument that context dependence is a tractable scientific problem when experiments are designed to separate both temporal and spatial sources of variation. Together, Chapters 3 and 4 provide complementary evidence. Chapter 3 demonstrates that interaction signals can shift through time and across ecological levels within one shoreline system, while Chapter 4 tests how those signals vary across environmental settings and identifies candidate moderators and community pathways that help explain why outcomes differ. This novel empirical foundation then motivates the thesis' final transition across the science–policy interface, where spatiotemporal management decisions must accommodate interacting stressors, context dependence, and uncertainty across sectoral and state jurisdictions.

Statement of Authorship

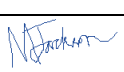
Title of Paper	Global Intertidal Community Responses to Warming and Nutrient Enrichment
Publication Status	□ Published □ Accepted for Publication ✓ Submitted for Publication □ Unpublished and unsubmitted work written in a manuscript style
Publication Details	Manuscript details Title: Global Intertidal Community Responses to Warming and Nutrient Enrichment. Status: In review at *Communications Biology*. • The submitted version within this thesis includes the material of the submitted manuscript (in peer review at the time of submission of corrections), alongside additional revisions following doctoral viva examination. Author list Ramesh Wilson, James Orr, Katie Driver, Fernando P. Lima, Jakob Thyrring, Khuong V. Dinh, Pamela A. Fernández, Maria Bagur, Markus Molis, Nicolas Moity, Ohad Peleg, João Canning-Clode, Christopher Cornwall, Hanh T. Dinh, João R. Nunes, Juan Vicente de Miguel, Minh-Hoang Le, Nadescha Zwerschke, Patrício Ramalhosa, Gretel Palma, Malena Pfoh, Rui Seabra, Soledad Álvarez, Henry C. Henson, João Barbosa, Laura Piazzese, Mar Humet, Ulrike Dietrich, Manfred Kaufmann, & Michelle Jackson. Data accessibility statement All datasets and analysis code supporting the findings of this study are archived at Zenodo (https://doi.org/10.5281/zenodo.18121701) and maintained in the associated GitHub repository. A derived land-cover raster used for land use summarisation is provided in the repository; the full global land-cover product is available from the Copernicus Climate Data Store (C3S/ESA CCI Land Cover) under its own licence and terms of use (https://cds.climate.copernicus.eu/datasets/satellite-land-cover; https://cds.climate.copernicus.eu/licences/satellite-land-cover). Daily weather time series were obtained from Visual Crossing under licence. Raw Visual Crossing downloads are not redistributed in this public archive as per terms of service; the derived weather summaries used in analyses are included. Raw weather data can be obtained directly from Visual Crossing subject to their terms (https://www.visualcrossing.com/weather-services-terms/).

Student confirmation

Student Name	Ramesh Wilson (RW)		
Contribution to the Paper	RW co-developed the project concept (with MCJ). RW led the study and constructed the experimental replicates, with support from KD, and with methodological input from FPL on intertidal temperature logging and experimental deployments. JT coordinated deployments across multiple northern sites. Field deployments, local logistics and sampling at individual global sites were organised and conducted by RW, JO, KD, FPL, JT, KVD, PAF, MB, MM, NM, OP, JCC, HTD, JRN, JVDM, MHL, NZ, PR, GP, MP, RS, SA, HCH, JB, LP, MH, UD and MJ, across respective sites. RW led the analysis, modelling, interpretation and synthesis of the work, with support from JO and MJ, and with additional water chemistry analytical contributions from KD, MK, HTD, KVD and PAF. RW wrote the full draft of the manuscript and led revisions, submission, and correspondence. Acknowledged non-author support: installation and sampling assistance (P. Sanders; B. V. Canh; F. Loayza; M. Castro; J. Miller; O. Florentin; J. Kaminsky); nutrient/water sampling (A. Bursztyn; P. Rodriguez; C. Laber); and permits/access enabled by relevant authorities and site administrations.		
Signature		**Date**	11/01/2026

Supervisor confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor Name and Title	Dr. Michelle Jackson (Associate Professor of Freshwater/Marine Ecology)		
Supervisor Comments	I certify that the candidate made a substantial contribution to the publication, and that the description described above is accurate.		
Signature		**Date**	11/01/2026

4.1 Abstract

Coastal ecosystems are subject to multiple human stressors, including nutrient enrichment and climate change. Their combined effects can deviate from simple additivity, hindering prediction and management. The same stressors can also produce different outcomes across environmental contexts, complicating generalisation. Progress therefore requires experiments that test multiple stressors in real-world seascapes and connect community change to underlying causal pathways, yet such studies remain rare. Here, we use a globally distributed intertidal field experiment across 22 rocky shore sites spanning 70° N to 55° S. We show that substrate warming reduces macroalgal cover and barnacle abundance, whereas nutrient enrichment increases both responses, with the abundance of motile grazing gastropods showing weaker responses. Pathway analyses indicate that warming affects barnacle abundance through both direct thermal stress and indirect pathways mediated by macroalgal cover. Local environmental context modified stressor impacts: nutrient enrichment effects on barnacles and grazers were strengthened in wet, high-runoff coasts, while air temperature variability amplified warming-driven declines in barnacle abundance. These findings position global trends as useful priors that require local interpretation to resolve context dependence. Taken together, they suggest that while warming sets broad constraints on coastal assemblages, managing nutrient inputs provides a tangible local lever to influence intertidal community responses under ongoing climate change.

4.2 Background

Human-driven stressors are driving rapid changes across terrestrial, freshwater, and marine ecosystems (Halpern et al., 2015, 2025; Jackson et al., 2016; Orr et al., 2020). Such stressor effects range from global-scale shifts such as warming, to local impacts such as nutrient enrichment, with stressors across different spatial scales often acting synchronously (Carrier-Belleau et al., 2021; Hodgson & Halpern, 2019). These co-occurrences can lead to interactive stressor effects, due to potential amplification or offsetting mechanisms, known as synergisms and antagonisms respectively (Jackson et al., 2021; Orr et al., 2020). Such interactions make it challenging to predict ecosystem responses and underscore the need for research to consider multiple stressors jointly to ensure effective management decisions (Kunze et al., 2021; Pansch & Hiebenthal, 2019).

In marine ecosystems, climate change and local anthropogenic stressors frequently intersect, with over 97% of the ocean simultaneously affected by more than one stressor (Halpern et al., 2015). Global climate change stressors such as warming, ocean acidification, and sea-level rise, operate across biogeographic scales and cannot be directly alleviated by local actions (Brown et al., 2013). Conversely, local stressors such as nutrient enrichment, land use change, or chemical pollution, act at site-specific scales and are amenable to direct intervention (Brown et al., 2013). Local conservation actions may help buffer ecosystems against more pervasive climate stressors, through enhanced resilience or recovery capacity (Carrier-Belleau et al., 2021). This has motivated recent efforts to better understand the effects of climate change and local stressors in tandem, and to inform 'climate-smart' management strategies that operate alongside global change (Frazão Santos et al., 2024).

Focusing on just one species or trophic level ignores the potential indirect impacts of stressors that can ripple throughout ecological networks of interacting species (Sarà et al., 2021). Indeed, climate change can intensify the impacts of local stressors at the species level, yet at the level of whole marine food webs or ecosystems, net stressor effects can sometimes be dampened or altered by ecological interactions and environmental feedbacks (Gissi et al., 2021). This underscores the necessity of synchronously observing key functional community groups to quantify the relative strengths of both direct stressor impacts *on* ecological groups,

and biotically mediated stressor impacts (e.g. predation, competitive exclusion, facilitation) between ecological groups.

Rocky intertidal ecosystems provide an excellent, tractable system for community-level, multiple stressor studies. Intertidal shores experience steep environmental gradients and support diverse communities of interacting organisms, including sessile filter feeders such as barnacles, benthic primary-producing macroalgae, and grazing invertebrates (Hawkins et al., 2020; Kunze et al., 2021; Micheli et al., 2016). These groups play critical ecological roles: for instance, barnacles create surface heterogeneity and varied microhabitats for other filter feeders and macroalgal settlement (Silva et al., 2015); macroalgae fuel food-web interactions and provide shelter and nursery habitat (Smale et al., 2013); and grazing invertebrates control macroalgal overgrowth, thereby mediating succession patterns (Branch et al., 2023). All three of these functional groups are ubiquitous across rocky shores worldwide, making them ideal indicators of global shoreline change (Hawkins et al., 2020; Mieszkowska et al., 2019). Changes in the abundance or relative composition of these groups can be indicative of broader ecosystem shifts, given their strong interdependence.

In the rocky intertidal zone, dynamic abiotic factors such as considerable heat and desiccation, extreme salinity fluctuations, or strong wave exposure could act as chronic stressors on local biota, even in the absence of added human influence (Kunze et al., 2021). These local context dependencies can profoundly influence sensitivities of intertidal biota to additional interactive human stressors (Helmuth & Hofmann, 2001; Micheli et al., 2016). By incorporating multiple spatial contexts into a comparative study, we can assess whether ecosystem responses to stressor effects are universal, or locally context dependent. However, most marine multiple stressor studies remain geographically narrow, with only ~6.5% spanning multiple biogeographic regions; the majority focusing on particular species or habitats, and with many emphasising 'explanatory' analyses of past impacts rather than anticipatory future scenarios (Gissi et al., 2021). Almost 70% of ocean multiple stressor studies are conducted in the Northern Hemisphere and further dominated by temperate regions, leaving high latitude areas poleward of ~60° scarcely examined, and the Southern Hemisphere underrepresented overall (Gissi et al., 2021; Thyrring et al., 2025). Understudied regions such as tropical and polar ecosystems are exceptionally important: tropical regions contain much of Earth's biodiversity, and polar systems are undergoing rapid climate-driven change (Barlow et al., 2018; Post et al., 2019). These taxonomic, habitat, and regional skews

create a substantial knowledge gap in forward-looking, large-scale assessments of how stressors interact across rocky intertidal communities.

Here, we adopt a global, ecological community approach by conducting a fully factorial, distributed field experiment across 22 rocky shore sites in 11 international locations across a large latitudinal gradient (Fig. 1). Our locations further spanned six climate zones across five continents, disparate land use contexts, and contrasting wave climates (Fig. 1; see Table 1 for detailed site classifications and Table 2 for seasonal wave descriptors; see also SI Fig. S1 for land use contexts). At each location, we deployed passively warmed (black) and ambient (white) settlement plates at paired nutrient-enriched and non-enriched rocky shores, to investigate whether the independent and interactive effects of simulated substrate warming and nutrient enrichment on barnacles, herbivorous grazing gastropods, and early-settling macroalgae are consistent globally, or vary across locations. We used generalised linear mixed models (GLMMs) to estimate global independent and interactive stressor effects, and meta-regressions to assess whether biogeographic and local environmental moderators explained between-site deviations from global means. Finally, we applied path analysis to partition direct stressor paths from indirect, biotically mediated pathways among community groups. By investigating both the direct and indirect effects of multiple stressors, we examine whether generalised patterns emerge, or whether local idiosyncrasies and biotic interdependencies mediate context-dependent stressor effects.

Within each of the 11 locations, we selected paired, categorically nutrient-enriched (mean proportional enrichment = +615% for nitrate (NO_3^-); +312% for phosphate (PO_4^{3-}); see Fig. 2 for site-level nutrient elevations; see Methods and Supplementary Methods (Experimental) for details on enrichment calculations) and non-enriched rocky shores, yielding 22 sites total globally (11 enriched, 11 non-enriched). At each site, we deployed 12 settlement plates at mid-tide (six black, six white; 264 total plates across all sites). Warming was manipulated passively by increased thermal absorption of black plates, with mean maximum temperature during tidal emersion elevated by +1.4 °C across all sites compared to ambient white plates (Fig. 1C; see Fig. 2 for site-level logger summaries; see Methods for further details on stressor verifications, data collection and analysis). Overall, we found that warming and nutrient enrichment consistently shifted community structure globally, with responses further conditioned by local context and community interdependencies.

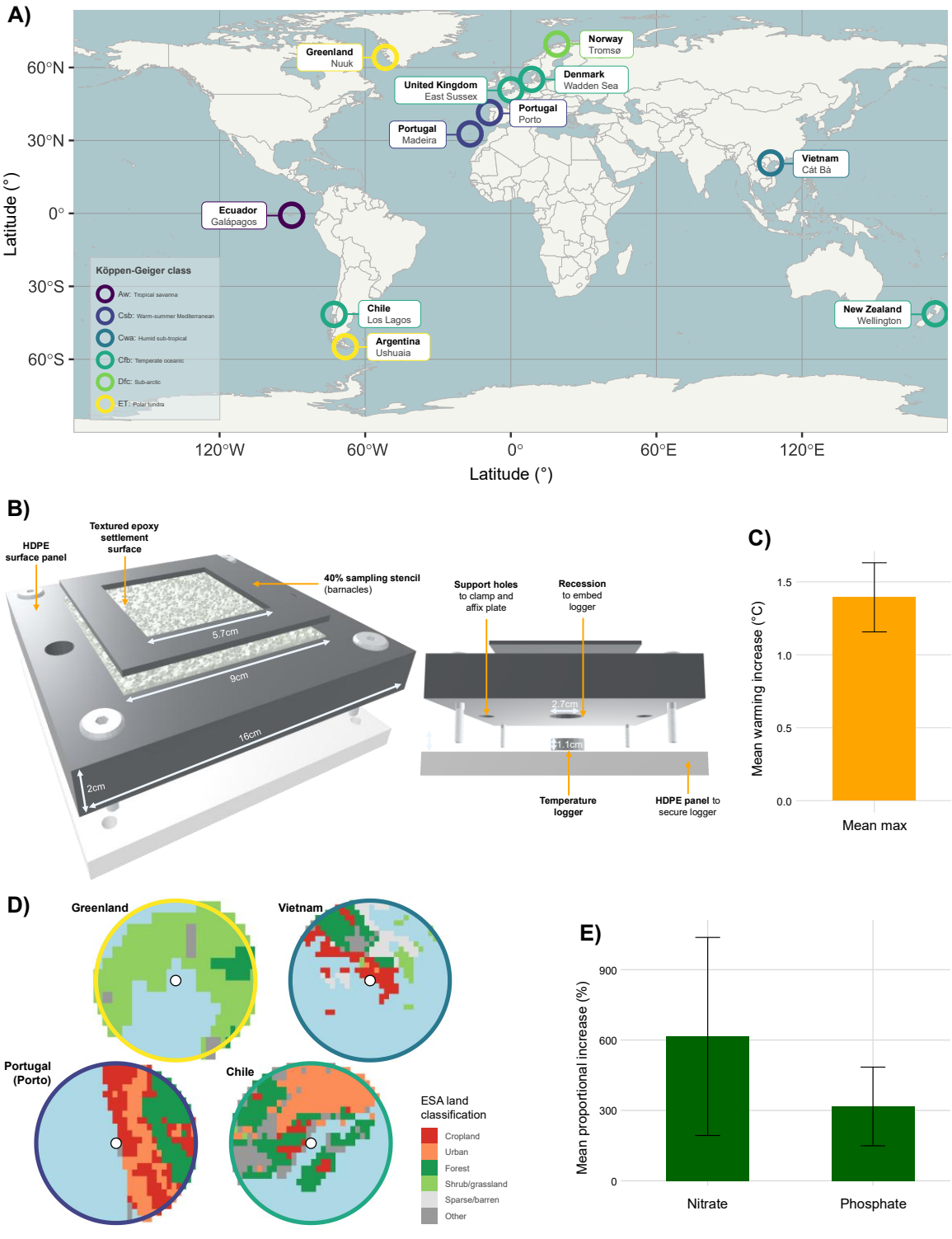


Figure 1 | Global experiment overview, methods, and site contexts. A) Map of 11 paired coastal locations (22 sites) coloured by Köppen–Geiger climate class (see Methods and Supplementary Methods (Experimental) for details on classification characteristics). Points mark the geodesic midpoint between each location's nutrient-enriched and non-enriched sites (coordinates in Table 1). B) 3D renderings of the black treatment plate (surface and underside) with key design features and dimensions (see Methods and Supplementary Methods (Experimental) for construction details). The textured epoxy area provides the settlement surface. C) Global mean of experimental plate warming, ΔWarming = warmed − ambient, computed from mean daily maximum plate temperature over the sampling window (°C). D) Example 5 km land cover context around four site midpoints (Greenland, Vietnam, Portugal (Porto), Chile). Land cover is from the ESA CCI 2022 product at 300 m spatial resolution (each pixel is one 300 m land cover cell) aggregated to six classes: Cropland, Urban, Forest, Shrub/grassland, Sparse/barren, and Other. The white point marks the geodesic midpoint, and the circle delineates the 5 km buffer used to compute % human-dominated land (cropland + urban) in subsequent analyses, colour-coded by the Köppen–Geiger classification of the respective location (full panels in SI Fig. S1). E) Global mean proportional nutrient enrichment for nitrate (NO_3^-) and phosphate (PO_4^{3-}) over the summer sampling period, computed from site-level summer means as % enrichment (see Methods). Error bars show ±1 SE across locations.

Location	Region	Enriched site (lat, lon)	Non-enriched site (lat, lon)	Midpoint (lat, lon)	Hemisphere	Continent	Köppen class	Köppen description	Aggregate climate zone
Argentina	Ushuaia	-54.8400, -68.3232	-54.8188, -68.1814	-54.8000, -68.2000	S	South America	ET	Polar tundra	Temperate
Chile	Los Lagos	-41.4962, -72.9855	-41.5943, -72.7050	-41.5000, -72.8000	S	South America	Cfb	Oceanic, no dry season, warm summer	Temperate
Denmark	Wadden Sea	55.0850, 8.5680	55.1460, 8.6060	55.1000, 8.5900	N	Europe	Cfb	Oceanic, no dry season, warm summer	Temperate
Ecuador	Galápagos	-0.7434, -90.3039	-0.7659, -90.3406	-0.7600, -90.3000	S	South America	Aw	Tropical savannah	Non-temperate
Greenland	Nuuk	64.1780, -51.7010	64.1670, -51.7460	64.2000, -51.7000	N	North America	ET	Polar tundra	Non-temperate
New Zealand	Wellington	-41.2380, 174.8970	-41.3206, 174.8706	-41.3000, 175.0000	S	Oceania	Cfb	Oceanic, no dry season, warm summer	Temperate
Norway	Tromsø	69.6442, 18.9520	69.6346, 18.9026	69.6000, 19.0000	N	Europe	Dfc	Cold, no dry season, cold summer	Non-temperate
Portugal 1	Madeira	32.6454, -16.9113	32.7414, -16.7140	32.7000, -16.8000	N	Europe	Csb	Mediterranean, dry-warm summer	Temperate
Portugal 2	Porto	41.5640, -8.7981	41.3096, -8.7426	41.4000, -8.7800	N	Europe	Csb	Mediterranean, dry-warm summer	Temperate
United Kingdom	East Sussex	50.7850, 0.0210	50.7890, -0.0020	50.8000, 0.0097	N	Europe	Cfb	Oceanic, no dry season, warm summer	Temperate
Vietnam	Cát Bà	20.7261, 107.0454	20.7402, 106.9974	20.7000, 107.0000	N	Asia	Cwa	Humid subtropical (monsoon), dry winter, hot summer	Temperate

Table 1 | Site list and classifications. For each coastal location (paired nutrient-enriched and non-enriched rocky shores), the table reports decimal-degree coordinates (lat, lon; WGS84) for each site and the geodesic midpoint between the pair (used for climate classification and catchment-context processing). Hemisphere is assigned from the midpoint latitude (N = north; S = south). Köppen code and description are the Köppen–Geiger climate class extracted at the midpoint from the Beck et al. (2023) 1991−2020 V2 map (0.01°). Aggregate climate zone bins sites by major Köppen group (Temperate = C; Non-temperate = all other classifications), except Ushuaia, which is extracted as ET but treated as Temperate (ET/Cfc transition; see Supplementary Methods (Experimental) for additional details).

Location	Region	Midpoint (lat, lon)	VHM0: Wave significant height (m)				VTM10: Spectral mean wave period from the inverse-frequency moment (s)			
			VHM0 Mean	VHM0 Median	VHM0 P90	VHM0 Max	VTM10 Mean	VTM10 Median	VTM10 P90	VTM10 Max
Argentina	Ushuaia	-54.8000, -68.2000	0.14	0.09	0.30	0.85	3.73	3.68	5.08	5.65
Chile	Los Lagos	-41.5000, -72.8000	0.17	0.10	0.45	0.91	2.76	2.61	3.73	7.68
Denmark	Wadden Sea	55.1000, 8.5900	0.91	0.75	1.75	3.34	4.87	4.89	6.29	8.73
Ecuador	Galápagos	-0.7600, -90.3000	1.09	1.06	1.37	1.76	9.72	9.77	11.65	13.95
Greenland	Nuuk	64.2000, -51.7000	0.57	0.47	1.01	3.03	5.46	5.45	6.77	9.37
New Zealand	Wellington	-41.3000, 175.0000	1.45	1.37	2.11	4.50	8.31	8.38	10.85	13.52
Norway	Tromsø	69.6000, 19.0000	1.29	1.12	2.13	4.45	7.66	7.60	9.40	11.66
Portugal 1	Madeira	32.7000, -16.8000	1.02	0.95	1.45	3.05	7.75	7.54	9.36	12.03
Portugal 2	Porto	41.4000, -8.7800	1.22	1.15	1.94	3.43	7.87	7.70	9.72	14.38
United Kingdom	East Sussex	50.8000, 0.0097	0.65	0.52	1.29	2.72	4.74	4.51	6.33	12.36
Vietnam	Cát Bà	20.7000, 107.0000	0.56	0.55	0.94	2.44	4.20	4.10	5.16	8.30

Table 2 | Seasonal wave-climate descriptors for each global study location. Wave context was characterised at the geodesic midpoint of each enriched and non-enriched site pair using the Copernicus Marine Global Ocean Waves Reanalysis product (GLOBAL_MULTIYEAR_WAV_001_032; dataset cmems_mod_glo_wav_my_0.2deg_PT3H-i). For each location, VHM0 represents sea surface spectral significant wave height (m) and VTM10 represents the sea surface spectral mean wave period from the inverse-frequency moment (s). Values shown are the mean, median, 90th percentile (P90) and maximum across the site-specific experimental summer window. Where the exact midpoint returned missing values due to coastal land–sea masking at product resolution, values were extracted from the nearest wet grid cell within a small bounding box around the midpoint.

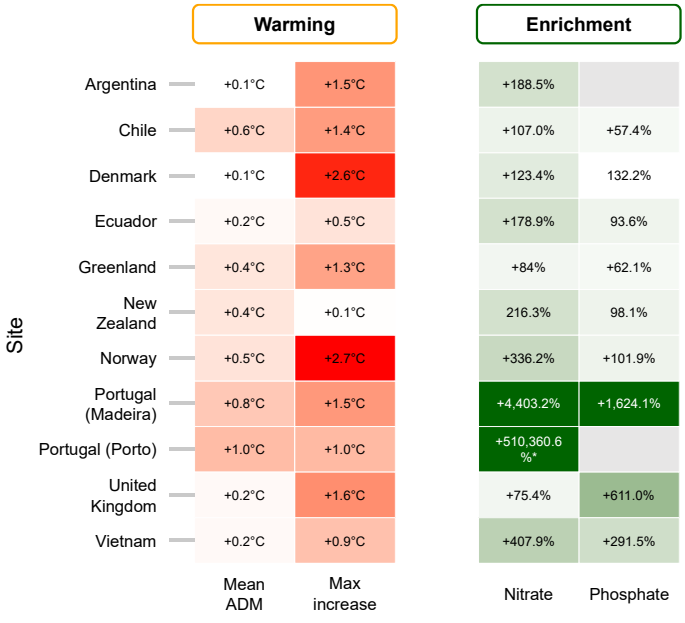


Figure 2 | Site-specific elevations in warming and enrichment during the sampling period. Warming is summarised from plate loggers as ΔWarming = warmed−ambient, computed using 1) ADM (average of daily maxima; mean of daily maximum plate temperatures over the sampling window, unadjusted for tidal immersion periods) and 2) Max (maximum plate temperature recorded over the sampling window; mean max across all sites shown in Fig. 1C). Enrichment is summarised as % enrichment for each site and nutrient as 100 × (E − NE) / NE*, with NE* = max(NE, ε). NE and E denote the non-enriched and enriched summer means, respectively, and ε (pseudo-count) is estimated per nutrient, employed only for proportional elevation calculations when non-enriched sites were extremely oligotrophic (NE ≈ 0), indicated with asterisks here (see Methods and Supplementary Methods (Experimental); proportional elevation across all sites shown in Fig. 1E). Sites lacking phosphate measurements are omitted for global PO_4^{3-} calculations and are indicated as grey tiles.

4.3 Main

4.3.1 Warming and nutrient enrichment independently shift community groups

We used generalised linear mixed models (GLMMs) to disentangle the independent and interactive effects of warming and nutrient enrichment on key functional community groups (see Methods and Supplementary Methods (Analyses) for details on model choices and interaction classifications). Across all sites, warming tended to reduce barnacle abundance (−45.6%, 95% confidence intervals (CIs): −75.1 to +18.8%, p = 0.082) whereas nutrient enrichment showed a positive, but non-significant response (+39.8%, 95% CI: −51.1 to +299.5%, p = 0.490). The interaction term was not significant (p = 0.548) and did not deviate significantly from the expected multiplicative-scale null model (i.e. additivity on the log scale; see Methods and SI Table S6 for global fixed-effect coefficients). When warming effects were estimated separately within non-enriched and nutrient-enriched treatments, barnacle abundance significantly declined under warming in both nutrient contexts, with similar effect sizes (non-enriched: −45.6%, 95% CI: −67.2 to −9.6%, p = 0.021; enriched: −53.0%, 95% CI: −69.3 to −28.1%, p = 0.002; see Fig. 3A and SI Table S7 for estimated marginal means (EMMs)). At the site level, most locations showed warming declines in barnacle abundance of −40% to −77%, with few CIs overlapping zero (Fig. 4A; SI Table S9A). Biogeographic comparisons showed no significant moderation of stressor effects independently or interactively by climate zone (Köppen climate classifications binned to temperate/non-temperate for statistical power; see Methods and Table 1) or absolute latitude (SI Tables S10A and S10B).

Warming also tended to reduce grazer abundance globally, but only on non-enriched plates (−13.6%, 95% CI: −26.5 to +1.6%, p = 0.077; enriched plates: p = 0.768) (Fig. 3B; SI Tables S6 and S7). Neither nutrient enrichment (p = 0.297) nor the interaction term was significant (p = 0.282), and the interaction effect did not deviate from the multiplicative-scale null model (i.e. additivity on the log scale; see Methods and SI Table S6). At the site level, warming effects on grazer abundance largely clustered around a decline of ~25% on average, whereas nutrient enrichment effects were more heterogeneous in sign and magnitude, and interaction effects for most sites were near zero, indicating little deviation from additivity on the log

scale (Fig. 4B; SI Table S9B). As with barnacle abundance, biogeographic comparisons showed no moderation of stressor effects on grazer abundance by absolute latitude. However, the interaction term significantly differed between climate zones: in non-temperate sites, the interaction effect was slightly negative (−6.3%), while in temperate sites it tended to be positive (+31.8%, t(8.22) = −2.79, p = 0.023) (SI Tables S10A and S10B). This interaction pattern is broadly consistent with potential thermal-performance expectations for many temperate grazers, which often operate below thermal optima; modest warming can increase metabolic and foraging rates, and when nutrient enrichment simultaneously boosts macroalgal quantity or quality, combined effects may compound, yielding a more positive effect on abundance than predicted by both stressors acting independently (Harley et al., 2006; Helmuth & Hofmann, 2001; Iannino et al., 2021). By contrast, the non-temperate grouping spans both tropical shores, where taxa may be closer to physiological limits, so additional warming may elevate maintenance costs and reduce feeding efficiency, and polar shores, where intertidal organisms experience wide temperature ranges and modest warming may initially relieve cold stress before approaching upper thresholds (Ashton et al., 2017; Sellers et al., 2021). Necessary aggregation of finer climate zones to temperate/non-temperate (see Methods) did not permit delineation of tropical and polar responses individually. However, overall, temperate sites show a clear positive interaction tendency compared to non-temperate sites. Moreover, these patterns are interpreted as the aggregated response of herbivorous plate-colonising gastropods, rather than the broader molluscan assemblage of each shore, which may also include non-herbivorous taxa not represented in this functional-group metric.

Macroalgal cover responded strongly to both warming and nutrient enrichment. Warming reduced macroalgal cover globally (−32.1%, 95% CI: −48.9 to −9.9%, p = 0.007), whereas nutrient enrichment tended to increase cover (+65.3%, 95% CI: −6.3 to +191.4%, p = 0.082). The interaction term was non-significant (p = 0.587) and did not deviate significantly from the odds-ratio-scale null model (i.e. additivity on the logit scale; see Methods and SI Table S6). When warming effects were estimated separately within non-enriched and nutrient-enriched sites, decreases in macroalgal cover were evident under both non-enriched (−32.2%, 95% CI: −48.9 to −9.9%, p = 0.007) and enriched conditions (−24.8%, 95% CI: −44.3 to +1.4%, p = 0.062). Similarly, when nutrient enrichment effects were estimated separately within ambient and warmed plates, nutrient enrichment increased macroalgal cover under warmed conditions (+83.1%, 95% CI: +3.1 to +225.2%, p = 0.039) and under

ambient warming conditions (+65.3%, 95% CI: −6.3 to +191.4%, p = 0.082) (Fig. 3C; SI Table S7). Site-level responses were heterogeneous; warming effects generally tracked the global decline of −32.1%, while nutrient enrichment effects were typically positive, but varied in magnitude (Fig. 4C; SI Table S9C). Neither climate zone nor absolute latitude significantly moderated stressor effects on macroalgal cover (SI Tables S10A and S10B). Because macroalgal cover was quantified on settlement plates over a single seasonal window, this response is most appropriately interpreted as early colonisation by opportunistic macroalgae rather than establishment or loss of mature perennial fucoid canopies. Accordingly, interactions with barnacles and grazers may differ from those expected on fully developed canopy-forming shores.

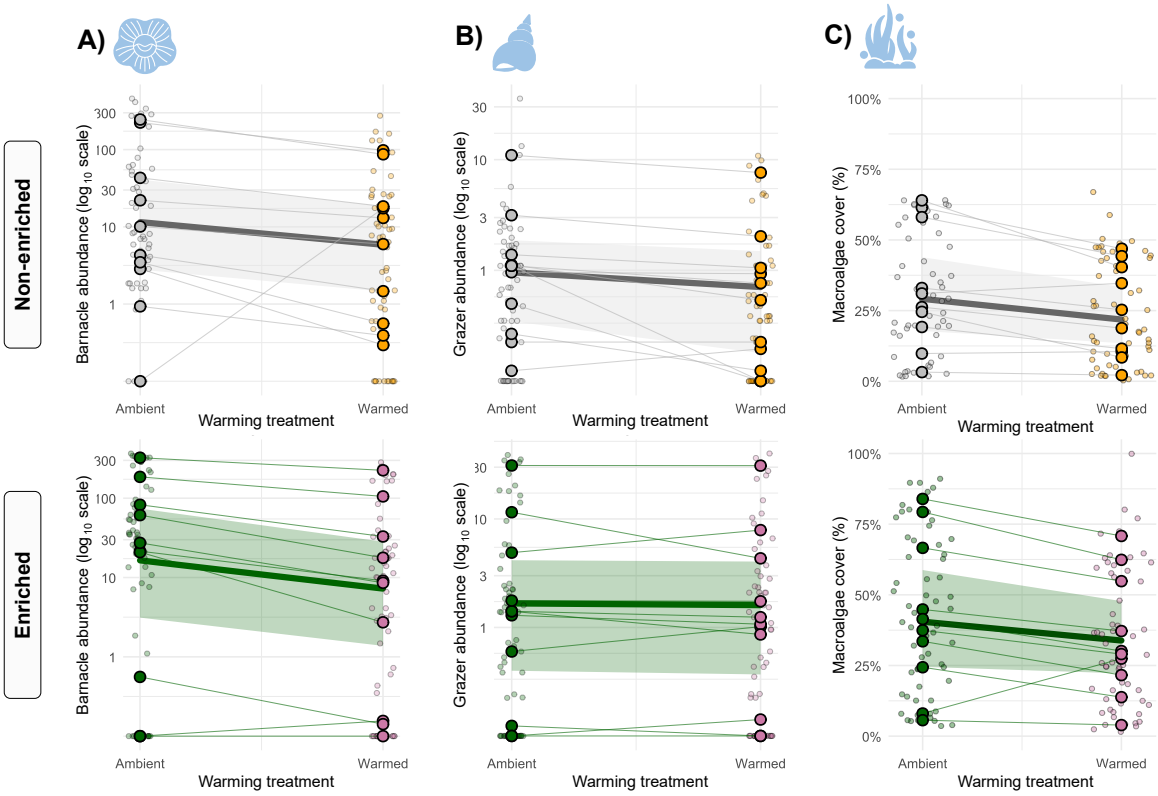


Figure 3 | Conditional effects of warming within nutrient enrichment strata for each response group. Model-predicted conditional means (estimated marginal means, EMMs) with 95% CIs for A) barnacle abundance, B) grazer abundance, and C) macroalgal cover under stressor combinations of warming and nutrient enrichment (see Methods and Supplementary Methods (Analyses) for model details). Within each column, the top panel shows non-enriched sites and the bottom panel shows nutrient-enriched sites, with the x-axis contrasting ambient vs. warmed plates. Small points show individual plate-level observations, coloured by treatment combination (grey = non-enriched + ambient; orange = non-enriched + warmed; dark green = enriched + ambient; pink = enriched + warmed). Larger circles represent site-level means, and thin lines connect paired means within sites, highlighting among-site variation. Thick regression lines and shaded ribbons show the fitted GLMM global mean predictions and 95% CIs (grey = non-enriched; dark green = enriched). For each response group, the non-enriched and nutrient-enriched panels are plotted on the same y-axis scale to enable direct comparison between nutrient contexts. Barnacle and grazer responses are plotted on a $\log_{10}$ scale y-axis to emphasise proportional changes across orders of magnitude; as $\log_{10}(0)$ is undefined, zeros and very low mean values appear at the lower axis limit rather than an explicit zero. Macroalgal cover is shown as percentage on the original 0−100% scale, with predictions back-transformed from the beta-logit GLMM to the data scale. Full EMM values are reported in SI Table S7.

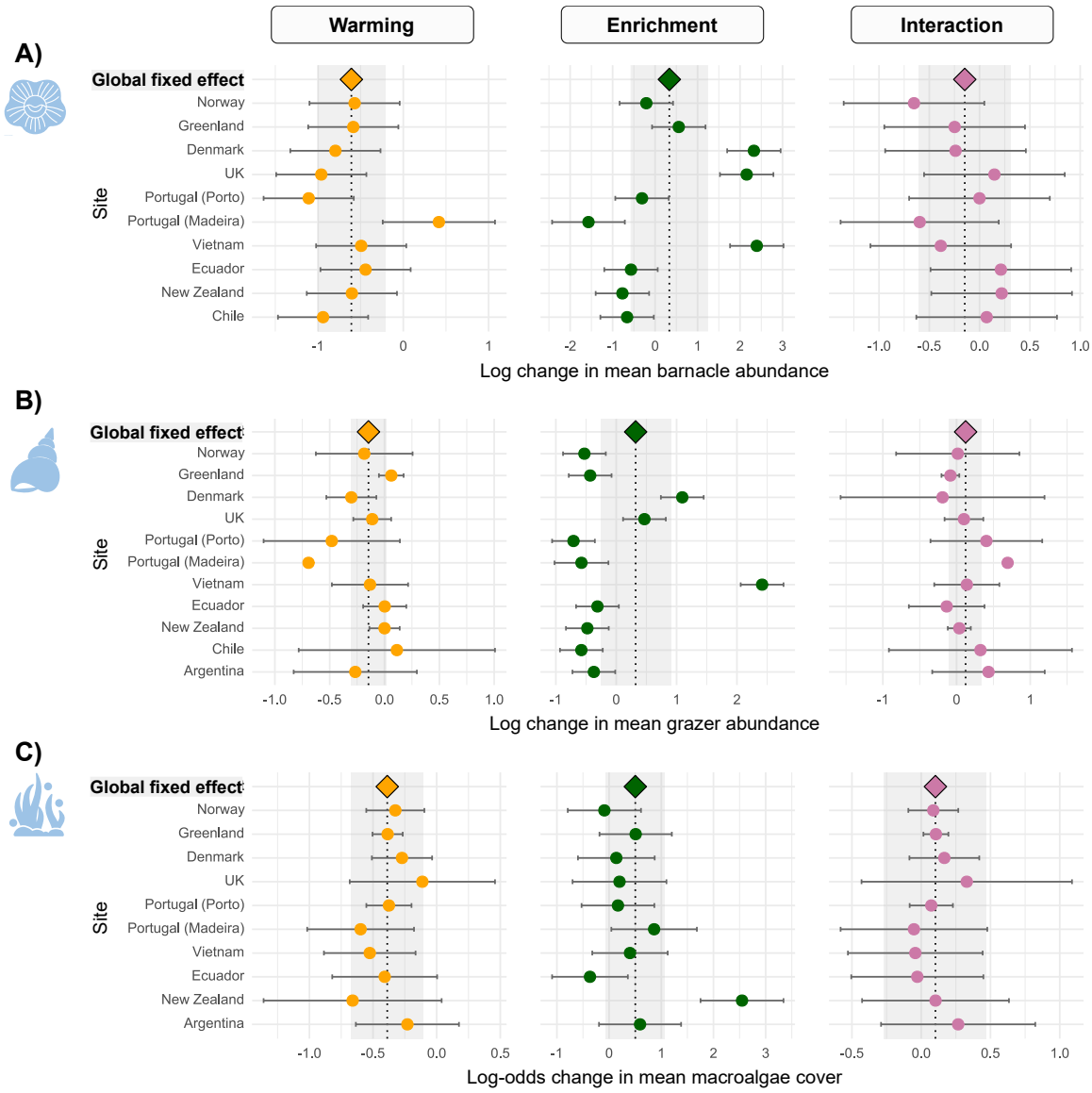


Figure 4 | Site-level deviations from global effects, ordered by absolute latitude (north to south). Points show per-site treatment effects on the link scale of the models (BLUPs: best linear unbiased predictions; see Methods): log-change in A) mean barnacle abundance and B) grazer abundance; C) log-odds change in mean macroalgal cover, expressed as percentage change for plotting. Horizontal bars show uncertainty. For barnacles and macroalgae, these are 95% CIs based on the conditional random-effect variance of the GLMM. For grazers, enrichment effects are BLUPs with model-based 95% CIs, whereas warming and interaction effects are empirical within-site contrasts plotted with Wald 95% CIs based on propagated within-site standard errors, as random slopes were not supported (see Methods). For the warming and interaction effects at the non-enriched Madeira site, replication was very low following plate detachments (see Supplementary Methods (Experimental)), so the propagated standard error is effectively zero, and the 95% interval collapses to the point. Dashed vertical lines highlight the global fixed-effect estimates, with grey shaded vertical ribbons representing their 95% CIs from the mixed models.

The pattern of warming-driven declines across functional groups is consistent with thermal and desiccation mechanisms during colonisation. Substratum warming raises body temperatures above air or water temperature via solar loading and conduction, which can limit macroalgal settlement at low tide, and constrain juvenile barnacle recruits during aerial exposure (Román et al., 2020; Wang et al., 2020). Observed reductions of grazers on warmed treatments likely reflect redistribution rather than mortality, with individuals shifting to

ambient substrates or potential nearby canopy refuges. In contrast, nutrient enrichment produced modest elevations in abundance across all groups; however, this effect was clearly significant only for macroalgal cover, particularly under warmed conditions, consistent with classic coastal subsidy pathways in which elevated nutrient and phytoplankton supply enhances filter-feeder performance and stimulates macroalgal growth where grazing does not fully counteract it (Iannino et al., 2021).

Interestingly, across all three functional groups, global interaction effects of combined warming and nutrient enrichment were statistically non-significant and did not deviate significantly from the expected null models. However, this pattern is consistent with syntheses of marine multiple stressor experiments at moderate stressor intensities, whereby additive or weakly antagonistic outcomes are common, and synergies tend to be rarer or emerge only under higher stressor intensities or when exposures align in time, though this remains context dependent across taxa and response type (King et al., 2022; Ostrowski et al., 2022). Fluctuating stressor regimes can also compress apparent interaction strength when averaged, even if organisms experience strong short-term impacts (Ostrowski et al., 2022). In our experiment, passive substrate warming was dependent on aerial exposure and scaled with ambient atmospheric temperature at low tide, while nutrient enrichment varied with local context and the timing and magnitude of nutrient pulses. These features likely contributed to the lack of significant deviations from the respective null models.

4.3.2 Local context mediates stressor effects

We next examined whether between-site deviations from the global fixed effects could be attributed to local context. We pre-specified a set of moderators based on mechanistic expectations, with thermal descriptors (e.g. magnitude of experimental warming, daily air-temperature variability) for warming effects, and hydrological and catchment variables (e.g. precipitation, land use, proportional nutrient elevation) for nutrient enrichment effects (see Methods for rationale, data sources, and transformations). Local environmental moderators had clear influences: atmospheric temperature variability shaped warming effects on barnacle abundance, and hydrological context mediated nutrient enrichment responses in barnacles and grazers (see Fig. 5 for core set of moderator outputs; full moderator outputs are shown in SI Figs. S3 and S4, and Tables S11–S13).

For barnacle abundance, there was no detectable association between the magnitude of experimental warming (ΔWarming, °C; see Fig. 2 for site-specific elevations) and the categorical warming response in non-enriched treatments (p = 0.926). Under nutrient-enriched conditions, however, the association between ΔWarming and the warming response was negative (r = −0.57, p = 0.083), suggesting proportionally greater reductions in barnacle abundance at enriched sites where plates experienced stronger warming (Fig. 5A); we interpret this result qualitatively given the statistical multiplicity of moderator tests (see Methods). Among other thermal moderators, the standard deviation (SD) of daily air temperature range was negatively related to the warming response (r = −0.67, p = 0.035), indicating stronger warming-driven barnacle abundance losses at more thermally variable sites (Fig. 5A). Mean daily maximum air temperature showed no detectable association, and we found no systematic effects of temperate versus non-temperate zone or absolute latitude. For grazer abundance, associations between ΔWarming and the warming response were weak and non-significant, while for macroalgal cover, they were positive but likewise non-significant; all other local thermal and biogeographic moderators similarly showed no clear effects on mediating site-level differences in grazer abundance or macroalgal cover in response to stressor treatments.

Across all groups, there was no evidence that the proportional elevation in nitrate in nutrient-enriched sites (i.e. compared to the non-enriched site of a given location; see Methods and Fig. 2 for site-specific elevations) moderated the categorical nutrient enrichment response in either warmed or ambient treatments. By contrast, precipitation covariates were positively related to the nutrient enrichment effect in two functional groups. Grazer abundance showed a strong positive association with mean precipitation (r = 0.98, p < 0.001), and barnacle abundance similarly showed a positive association (r = 0.64, p = 0.063) (Figs. 5A and B). No local moderators were statistically significant for macroalgal cover. Notably, for barnacles and grazer abundance, the precipitation moderator signal was highly sensitive to the inclusion of the Vietnamese site, which experienced anomalously high rainfall (see Figs. 5A and B); leave-one-out cross-validation (LOOCV) checks indicated that estimates remained positive in sign but lost precision and are statistically non-significant when Vietnam is excluded (see Supplementary Methods (Analyses) for further information and SI Tables S13A and S13B for post-hoc sensitivities and diagnostics).

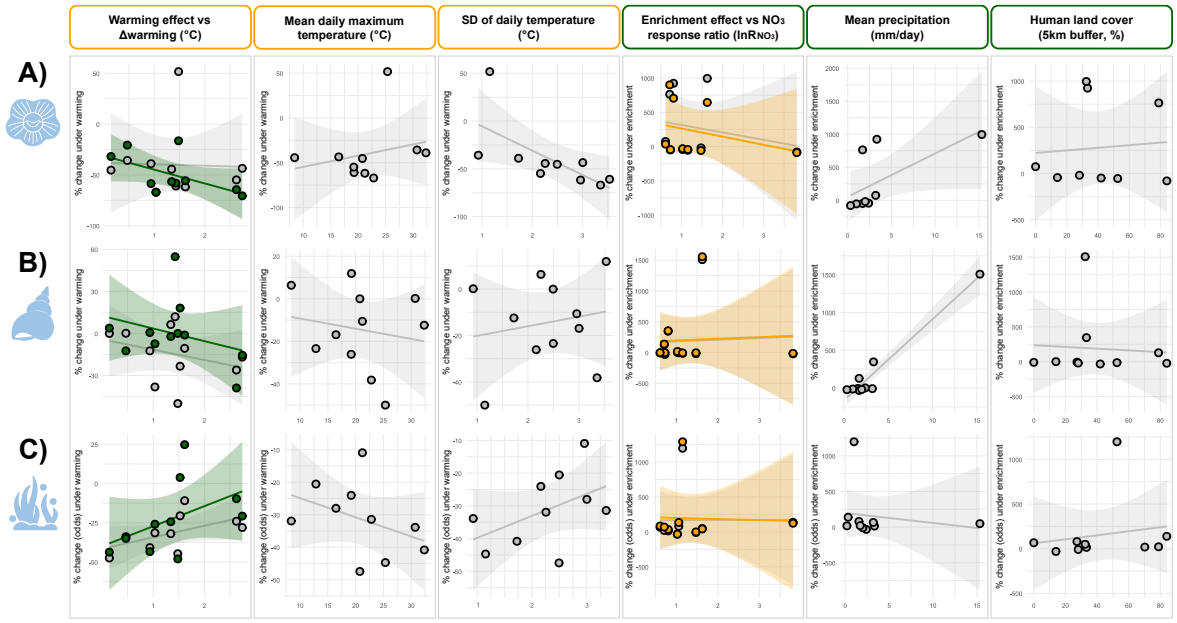


Figure 5 | Local environmental context mediates stressor effects. Rows are response groups: A) barnacle abundance; B) grazer abundance; C) macroalgal cover. Columns show local moderators used in meta-regressions: 1) warming effect versus ΔWarming (°C); 2) mean daily maximum air temperature (°C); 3) SD of daily air temperature range (°C); 4) enrichment effect versus nitrate response ratio $lnRNO_3$ (= ln[enriched/non-enriched]); 5) mean precipitation (mm/day); 6) human land cover within 5 km (%). Points are site-level effect estimates; lines are unweighted OLS fits with 95% CIs; effect sizes are back-transformed to % change in the mean (barnacles, grazers) or % change in odds (macroalgae). All other outputs (including broader biogeographic moderators), diagnostics, and validations are provided in the SI (Figs. S3 and S4; Tables S11–S13). For warming moderators (columns 1–3; orange column headers), only column 1 shows nutrient-enriched and non-enriched sites (see Methods): dark green point fills (and fit/ribbon) = nutrient-enriched sites; grey fills (and fit/ribbon) = non-enriched sites. Columns 2−3 show the non-enriched baseline only (grey fit/ribbon). For enrichment moderators (columns 4−6; dark green column headers), only column 4 shows warmed and ambient treatments separately (see Methods): orange fills (and fit/ribbon) = warmed plates; grey fills (and fit/ribbon) = ambient plates. Columns 5−6 show the ambient baseline only (grey fit/ribbon).

Together, the strong site-level deviations from global mean stressor effects (Fig. 4) and the moderator analyses (Fig. 5) show that warming and nutrient enrichment effects are strongly context-dependent. Hydrological setting mediated enrichment outcomes for barnacle and grazer abundance (Figs. 5A and B), consistent with rainfall-driven nutrient delivery that can boost filter feeders and intensify grazer control on macroalgae during high-runoff periods (Glibert, 2020). Furthermore, in cold regions, freshwater inputs can also derive from snow and ice melt rather than rainfall per se, potentially altering nutrient flushing and dilution in ways not fully captured by precipitation moderation alone; such processes may contribute to variance at polar sites. Contemporary assessments indeed link precipitation to elevated riverine nitrogen export and coastal eutrophication responses (Sinha et al., 2017). However, in our dataset the clearest signal came from one persistently wet site (Vietnam), and the moderation of nutrient enrichment effects by precipitation weakened and lost statistical significance when that site was excluded. This suggests that enrichment effects on barnacle and grazer abundance may be mediated by precipitation in notably high-rainfall contexts, but that this pattern may not reflect a universal effect. Short-timescale thermal context also mattered (Figs. 5A and B): broader diel temperature ranges amplified warming-driven losses

of barnacle abundance, consistent with thermally volatile sites more frequently pushing organisms beyond possible physiological limits of thermal intensity and duration. This pattern matches work on intertidal microclimates and exceedance-based heat-stress metrics, where the frequency and length of excursions beyond tolerance limits better predict damage than mean conditions alone (Román et al., 2020; Wang et al., 2020). Overall, these moderator patterns show that fine-scale local environmental conditions strongly shape how warming and nutrient enrichment effects propagate through invertebrate communities.

4.3.3 Direct and indirect biotic pathways connect stressors to community change

Our findings establish mean shifts of functional groups globally in response to warming and nutrient enrichment, and context dependence of stressor effects. Here, we investigate both 'direct' effects of stressors alongside 'indirect' effects propagated through biotic interactions. Our structural equation model (SEM; see Methods) showed that warming directly reduced both macroalgal cover ($\beta_{std} = -0.100$, $p < 0.001$) and barnacle abundance ($\beta_{std} = -0.238$, $p < 0.001$), whereas nutrient enrichment showed a positive direct effect on macroalgal cover ($\beta_{std} = +0.173$, $p = 0.066$) and no clear direct effect on barnacle abundance ($\beta_{std} = +0.128$, $p = 0.337$) (Fig. 6). A strong, negative macroalgal cover → barnacle abundance biotic path ($\beta_{std} = -0.358$, $p < 0.001$) indicates competitive suppression, consistent with space pre-emption by macroalgae. Furthermore, the best-fitting SEM (see Methods) included a residual negative correlation between barnacle and grazer abundance (standardised covariance = −0.122, $p = 0.026$), not captured by modelled directional paths (see Methods) (Fig. 6). In this SEM, the grazer node represents aggregated herbivorous gastropod abundance on the plates, rather than all molluscan taxa present in the wider shore system, and the macroalgal node represents taxonomically aggregated plate-settling macroalgal cover rather than species-resolved canopy composition. This modelled covariance possibly reflects unmeasured microhabitat processes, such as localised bulldozing or dislodgement of barnacle recruits by grazers, or small-scale spatial segregation where dense barnacle matrices and associated roughness alter grazer movement and create refuges for macroalgae from grazing (Ellrich et al., 2020; Silva et al., 2015).

Indirect, biotically mediated effects were prevalent (see Methods for details on indirect effect quantification). Positive macroalgae-mediated effects of warming on barnacle abundance

(warming → macroalgal cover → barnacle abundance) were shown (β_{std} = +0.036, 95% CI: +0.017 to +0.064), indicating partial offsetting of the direct negative warming effect on barnacle abundance. This is consistent with competitive release: because macroalgal cover suppresses barnacle abundance (Fig. 6), warming-driven reductions in macroalgal cover relax space pre-emption and partially counteract direct warming-associated losses of barnacles (Cervin et al., 2004; Jenkins et al., 1999). However, the total (direct + indirect) warming effect on barnacle abundance remained negative (β_{std} = −0.202, 95% CI: −0.340 to −0.161). Conversely, the indirect nutrient enrichment → macroalgal cover → barnacle abundance effect was negative (β_{std} = −0.062, 95% CI: −0.163 to −0.004), indicating that enrichment-driven macroalgal increases can suppress barnacle abundance via competition for space. Fixed effects explain a modest share (especially for grazer abundance), and there was substantial site-level heterogeneity (full outputs in SI Tables S14A and S14B).

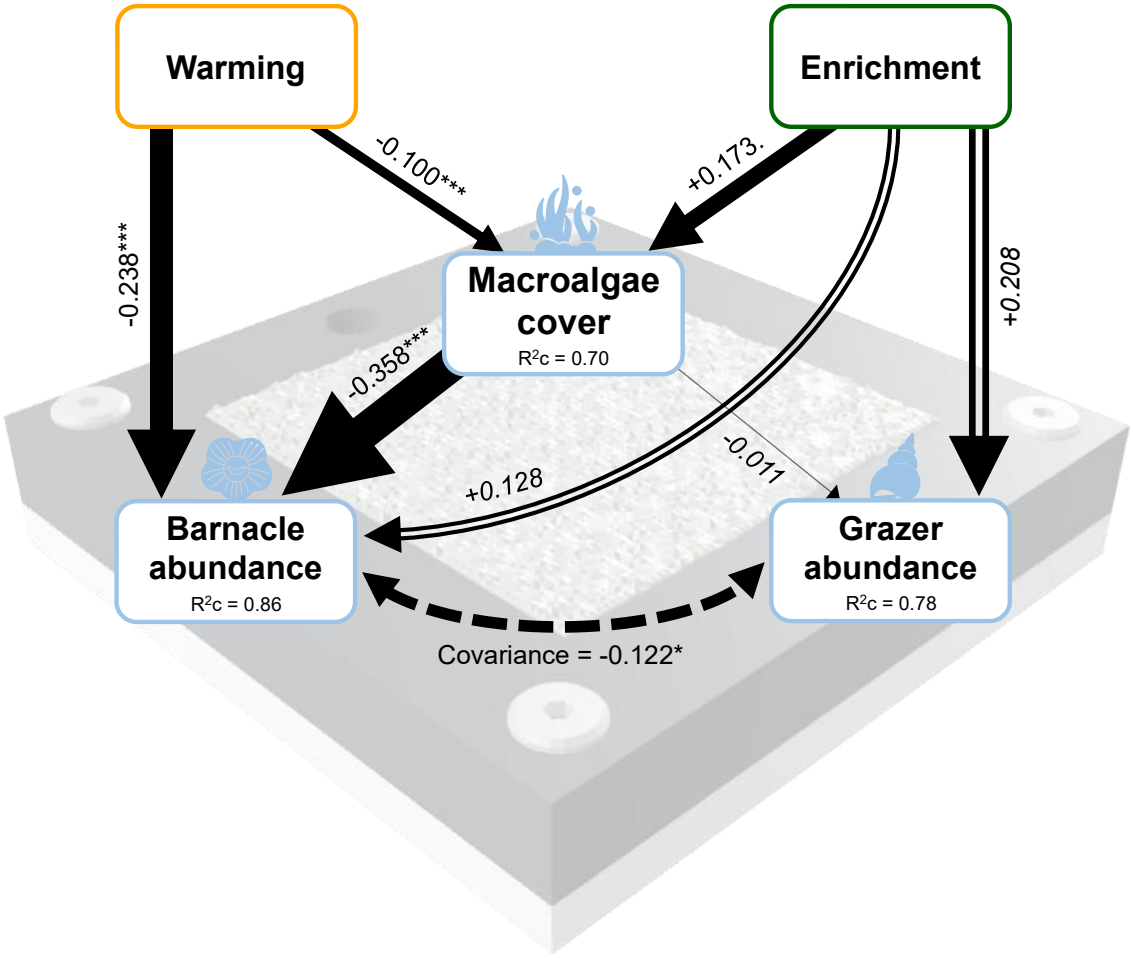


Figure 6 | Structural equation model linking stressors to community groups. Diagram shows directed paths (single-headed arrows) from warming and nutrient enrichment to macroalgal cover (beta-logit), barnacle abundance (log(count + 1)), and grazer abundance (log(count + 1)), plus a residual barnacle abundance ↔ grazer abundance covariance (dashed, double-headed arrow; see Methods and supplementary methods (analyses)). Arrow labels are standardised (z-score) path coefficients (β_{std}) with significance coded as: '***' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$; '.' $0.05 \leq p < 0.10$. Hollow arrows indicate $p \geq 0.10$, with arrow widths scaled to effect size. Boxes report conditional R^2 values (R^2c; fixed + random effects) for each endogenous node (see SI Table S4 for marginal and conditional values). Absolute fit was assessed using Shipley's d-separation test (Fisher's C): the SEM including the barnacle abundance ↔ grazer abundance covariance fit adequately (C = 4.14, df = 2, $p = 0.126$, i.e. independence claims are not rejected at $\alpha = 0.05$), whereas the reduced model without this covariance showed misfit (see SI Table S5 for d-separation tests). Sample sizes: macroalgal cover 10 locations (plate $n = 233$); barnacle abundance 10 locations ($n = 233$ plates); grazer abundance 11 locations (plate $n = 257$). Indirect and total effects, along with unstandardised coefficients, are reported in SI Tables S14A and B.

The SEM reveals indirect biotic pathways by which the same substrate warming and nutrient enrichment effects propagate through the community. We detect direct thermally driven losses of macroalgae, an enrichment-linked tendency for higher early-settling invertebrate abundance, and indirect effects in which stressor-driven shifts in macroalgal cover and invertebrate abundance modify competition for primary substrate, consistent with classic research on rocky-shore dynamics (Filbee-Dexter & Wernberg, 2018; Sellers et al., 2021; Spiecker & Menge, 2024). These patterns align further with syntheses showing that warming and marine heatwaves weaken foundational species and shorten macroalgal canopy dominance, opening settlement windows for turf algae and early invertebrate colonisers (Filbee-Dexter & Wernberg, 2018; Smale et al., 2019; Wernberg et al., 2016). Moreover, by partitioning direct and indirect pathways, the SEM helps explain why fixed-effect coefficients in our univariate GLMMs (i.e. global stressor effects) may appear modest on any single functional-group response: part of the stressor signals are transmitted through consumer and competitor nodes through indirect biotic paths, so joint, cumulative effects are expressed most clearly at the network level rather than solely as univariate responses (Schrodt et al., 2025).

4.3.4 Biogeographic context and mechanistic hypotheses

Two broad families of biogeographic mechanisms may help explain variation in functional-group responses to stressor effects across our experimental sites. First, bottom-up supply differs by coast, so the nutrient enrichment contrast between sites can translate into very different food contexts for intertidal communities. In river-influenced coastal regions where catchments deliver large nutrient loads to the sea (e.g. North Sea and Baltic shorelines), legacy nutrient inputs and episodic flood pulses can boost filter feeders and, where consumers are abundant, intensify top-down control of macroalgae (van Beusekom et al., 2019), consistent with the generally positive enrichment responses we observed in northern Europe (Fig. 4A and B). Monsoon-wet embayments (e.g. the Gulf of Tonkin) experience frequent nutrient pulses and plume retention following the East Asian summer monsoon (Nguyen-Duy et al., 2021), aligning with observed precipitation moderation in our study and the leverage of the Vietnam replicate in the strength of this signal (Figs. 5A and B).

Second, background oceanography can compress, invert, or redirect nutrient effects. Upwelling cycles off northwest Iberia and in the eastern tropical Pacific operate on broad timescales and can modulate whether nutrient-rich plumes are retained nearshore or

advected offshore (Picado et al., 2023), consistent with mixed-sign nutrient enrichment effects across taxa and wide site-level spread in our Portuguese sites (Fig. 4). Moreover, in the eastern tropical Pacific, near-coastal and equatorial upwelling around Ecuador and the Galápagos seasonally and interannually modulates temperature and nutrient baselines (Borbor-Cordova et al., 2019), which may help contextualise negative barnacle responses to nutrient enrichment at some South American sites in our network (Fig. 4A).

Additional innate characteristics at the local scale plausibly shaped variation of functional-group responses to stressors at individual shores. Public accessibility and trampling can suppress macroalgae and alter grazer assemblages; predator cues and direct predation by gastropods can reduce barnacle recruitment and survival; and co-occurring pollutants from sewage effluent (e.g. pharmaceutical mixtures) can restructure communities in ways not captured by warming and nutrient contrasts (Huguenin et al., 2019; Meyer et al., 2019).

4.3.5 Management implications and outlook

Climate forcing operates broadly across coasts, yet expression at any single shore is filtered by local context. Operationally, our results suggest a practical sequence for place-based management, whereby global trends can be treated as priors, then diagnosed locally with site-specific mediators that route impacts to habitats. This can then be accompanied by seascape-aware, connectivity-informed actions tailored to local conditions, and diagnostics of hydrology, oceanography, consumer pressure, and co-occurring stressor effects (Brown et al., 2013; Wedding et al., 2025). For monitoring, this argues for more systematically pairing measurements of physical and chemical stressors alongside environmental mediators that transmit effects to key functional groups, rather than tracking drivers alone. Intertidal organisms respond to body temperatures shaped by microhabitat, tidal timing, and substratum properties rather than simply mean air temperature (Helmuth & Hofmann, 2001; Wang et al., 2020), so exceedance-style heat metrics and targeted microclimate logging at sentinel sites can provide more decision-relevant signals than coarse atmospheric averages. In practice, such approaches will be more feasible at a subset of representative shores, where local substrate colour, shading, and tidal emersion patterns can be explicitly considered.

A near-term management priority suggested by our results and the wider literature is to curb nutrient pulses in high-runoff settings, where enrichment can coincide with stronger consumer presence and indirect suppression of macroalgal cover. Precipitation variability

and extremes are already associated with elevated riverine nitrogen delivery to coasts in many catchments, amplifying eutrophication risk and harmful algal blooms (Sinha et al., 2017). Operationally, managers can set locally specific triggers that open short management 'windows' following intense storms or heat events, align nutrient controls with wet-season peaks, and use cumulative-effects tools to weigh trade-offs among uses. Where financial and logistical capacity are limiting, sites can be targeted where diagnostics indicate high leverage: thermally variable shores for warming impacts, and rainfall-intensive basins for enrichment impacts as evidenced in this study. Furthermore, expectations should be set by interaction type to ensure efficacy. Although we did not detect significant global interactions between warming and enrichment on functional groups, broader syntheses suggest that synergies become more evident at higher intensities or when exposures align in time (Ostrowski et al., 2022). Local actions should therefore be aligned with climate-adaptation planning: cumulative human pressures on marine systems are widespread and increasing in intensity and frequency across many regions (Halpern et al., 2015, 2025), and reducing local loads can yield tangible ecological benefits under a range of future warming scenarios. Such actions fit naturally within anticipatory 'climate-smart' spatial planning which links land-based pressures to coastal ecological status, and requires cumulative effects analysis across economic sectors (Frazão Santos et al., 2024). Furthermore, embedding harmonised experimental methods as demonstrated in this study, within existing monitoring networks can deliver comparable ecological indicators across sites and both current and anticipatory stressor scenarios, while strengthening feedbacks between science and management. More broadly, globally distributed, standardised field experiments can complement conventional local studies by providing a tractable way to generalise ecological patterns while explicitly resolving context dependence across regions, supporting climate-smart coastal planning under both local and global change.

4.3.6 Conclusions

This study delivers a novel, *in situ* factorial experiment of multiple stressors across a global distribution of rocky shores, implemented with harmonised, low-cost instrumentation that links stressor effect sizes, biotic pathways, and local context moderation. This addresses a prominent gap in multiple stressor research, where global, manipulative studies remain scarce (Gissi et al., 2021).

Our distributed experiment shows that modest substrate warming erodes macroalgal cover and barnacle abundance, while nutrient enrichment tends to elevate these functional groups. Local context dependence was prominent: wet, high-runoff coasts tended to show stronger enrichment effects on barnacle and grazer abundance, with the clearest signal arising from a persistently wet, monsoon-influenced site, and broader diel air temperature ranges amplified warming-driven losses of barnacle abundance. Path analysis further indicated that competitive and consumer-mediated biotic pathways redirect a substantial portion of stressor impacts. Longer-term experiments are needed to determine how these indirect pathways evolve as communities mature and ecological feedbacks develop.

These results indicate that global mean responses to warming and nutrient enrichment are useful priors, but that local-scale environmental context and biotic community interactions can substantially alter realised effects. This study further demonstrates the practical feasibility of in situ experimental multiple stressor methodologies that can be deployed at wide spatial scales. If embedded within existing monitoring frameworks, similar experimental approaches could help translate broad stressor effect trends into locally specific diagnostics and management options, strengthening the link between global change and practical coastal decision-making.

4.4 Materials and methods

4.4.1 Experimental design

Our experiment spanned 11 coastal locations across five continents and six climate classifications, encompassing a broad range of coastal settings, climatic regimes, and wave climates (Fig. 1; Tables 1 and 2). Climate zones were assigned by extracting the Köppen–Geiger code at each pair's geodesic midpoint using the 1991–2020 global map of Beck et al. (2023). Wave exposure was additionally characterised descriptively for each location using the Copernicus Marine Global Ocean Waves Reanalysis product, extracting significant wave height (VHM0) and mean wave period (VTM10) at the geodesic midpoint of each enriched/non-enriched pair over the corresponding experimental summer window. Details on site selection are provided in the Supplementary Methods (Experimental).

To test for the effect of warming, we constructed settlement plates using black (warmed) or white (ambient) high-density polyethylene (HDPE) plastic (Fig. 1B). Each plate was topped with textured epoxy to mimic rocky substrate for community settlement. Black plates increased thermal absorption, raising seasonal mean daily maximum plate temperature by +1.4 °C (see Fig. 1C for global elevations; per-location summer logger elevations in Fig. 2). Full design and construction details are provided in the Supplementary Methods (Experimental).

Nutrient-enriched sites were chosen where dissolved inorganic nitrate (NO_3^-) and phosphate (PO_4^{3-}) were categorically higher than nearby non-enriched shores (see Fig. 1E for global mean enrichment elevations; per-location summer nutrient contrasts in Fig. 2). To quantify the magnitude of enrichment over the summer sampling window, we first averaged all nitrate and phosphate measurements at each location's enriched and non-enriched sites to obtain site-level summer means. We expressed enrichment as proportional percent increase: percent enrichment = $100 \times (E - NE) / NE^*$, where E and NE are enriched and non-enriched means, respectively, and NE* is equal to the larger of NE, or in discrete cases, a data-adaptive pseudo-count, ε (defined in the Supplementary Methods (Experimental); see also Fig. 2). This ε was used only when $NE \approx 0$, to avoid subsequent artificial inflation of proportional increases. In practice, ε was triggered for one nitrate site (Portugal 2 (Porto)), which produced an extremely large apparent proportional increase; this site was excluded from the global mean nitrate summary to avoid distorting the average.

We made three *a priori* design choices to preserve comparability of effects between sites. First, we classified each site's climate using the Köppen system and then aggregated these into 'temperate' and 'non-temperate' bins (see Table 1). This aggregation was necessary to maintain statistical power, as finer Köppen classes would yield groups with $n \approx 1$ for several categories. The non-temperate class therefore includes both tropical and polar/sub-polar sites and should be interpreted as a pragmatic grouping for statistical analysis rather than a strict ecological niche category. Second, we summarised logger data/time series using daily maxima (not average-of-daily-mean temperature; see Fig. 2): immersion/splash provide thermal relief in the intertidal, so averaging over submerged periods can underestimate biologically relevant heat exposure and exceedance. Third, we expressed nutrient contrasts as proportional response ratios or percent changes (see Fig. 2) rather than absolute concentrations, providing scale-free comparisons of enrichment effects across innately

oligotrophic, mesotrophic, and eutrophic contexts (see above and Supplementary Methods (Experimental) for further details).

Installations preceded each hemisphere's summer sampling by 5−6 months to allow early successional community colonisation following schedules adopted by previous *in situ* warming experiments on rocky shores (Kordas et al., 2015; Kordas & Harley, 2016). Southern plates were deployed June−July 2023 and sampled December 2023−March 2024. Northern plates were deployed January−February 2024 and sampled June−September 2024; the only exception was the UK, which was conducted a year prior (2023). All plates were installed at mid-tide to standardise biotic zonation, exposure, and warming potential. Sampling was carried out in the summer to maximise thermal absorption of settlement plates, as documented in existing studies (Kordas et al., 2015; Kordas & Harley, 2016). Additional schedule and installation notes are provided in the Supplementary Methods (Experimental).

4.4.2 Sampling and data collection

Sampling was conducted fortnightly, with a target of eight sampling dates throughout the season. Due to logistical constraints for some sites, most achieved 6−8 dates (see Supplementary Methods (Experimental)). At each sampling date, three community groups were measured: 1) barnacle abundance; 2) grazing gastropod abundance; and 3) macroalgal cover. Here, grazer abundance refers to herbivorous plate-colonising gastropods, whereas macroalgal cover refers to plate-attached early-settling macroalgae on the epoxy settlement surface.

Barnacle populations were counted using a 3D-printed stencil, sampling 40% of the epoxy region to avoid edge effects (Fig. 1B) (Kordas et al., 2015). Plates with very low densities (≤ 10 individuals) were counted *in situ*. In all other cases, overhead photographs were taken, and analysed using the mobile application CountThings. A convolutional neural network trained on acclimation and early-season images identified barnacles and opercula to distinguish living from dead individuals. Further details on model specifications, training, and thresholds employed by CountThings are provided in the Supplementary Methods (Experimental). Grazer populations were counted *in situ* and refer here to mobile herbivorous gastropods colonising the plates; predatory gastropods were not included in this functional group. Grazers indiscriminately colonised all surface and lateral side faces of the plates, irrespective of the rough epoxy settlement surface or smooth HDPE plate texture. Counts were therefore

conducted for both surface and side faces, and subsequently aggregated. Macroalgal cover was measured from overhead photos of the epoxy area and reflects plate-attached early-settling macroalgae on the settlement surface, rather than mature perennial canopy structure. Cover estimates were checked to ensure attachment to the textured surface, rather than loose detritus. Images were analysed in ImageJ with colour-thresholding to produce a binary (black/white) mask and percent cover (see the Supplementary Methods (Experimental) for workflow).

Loggers recorded plate temperature every 90 min at 0.1 °C resolution before and throughout the experiment. At each sampling date, measurements of water nutrient content (at enriched and non-enriched sites) were collected for nitrate and phosphate, using either *in situ* probes or laboratory assays, depending on local availability and resources (see Supplementary Methods (Experimental) for full details on monitoring and quantification). Biogeographic context was indexed by climate classification (temperate vs. non-temperate; see above) and absolute latitude from the equator. Local environmental context was characterised from daily weather readings at each location's geodesic midpoint (midpoint between enriched and non-enriched sites; see Fig. 1 for midpoints, and Table 1 for full coordinates) over the summer sampling period, accessed from Visual Crossing. Key candidate metrics were subsequently used in meta-regressions defined by causal reasoning (see Supplementary Methods (Analyses)). A full list of raw and derived weather variables from daily series can be found in Supplementary Table S1. Additionally, human land use within a 5 km radius of the geodesic midpoints was estimated from the ESA CCI Land Cover 2022 global product. We computed the percentage of 'human-dominated' land cover classes (cropland + urban). Full processing details and site panels are provided in SI Fig. S1.

4.4.3 Statistical analyses

Statistical analyses were run in R version 4.4.3.

Generalised linear mixed models (GLMMs)

Biotic responses were aggregated and averaged over the summer at each site, yielding one mean value per plate within each treatment for each functional group (barnacle abundance, grazer abundance, macroalgal cover). Sampling intervals and the total number of visits differed slightly among sites, and responses can reflect short-lived transient effects that are not the focus of this study. Aggregating to a seasonal mean therefore uses all within-season

observations, avoiding undue influence of any idiosyncratic time points. Further details are provided in the Supplementary Methods (Analyses).

We fitted GLMMs with fixed effects of warming, nutrient enrichment, and their interaction, and a random intercept for site nested within country. For each response, we excluded locations where the focal taxon was entirely absent across all plates and sampling dates. In such cases, treatments cannot create contrasts as there is no estimable baseline, so they do not inform stressor effects. Barnacle and grazer abundances were log-transformed and modelled with Gaussian LMMs to stabilise variance and to test interaction additivity on the log scale (i.e. a multiplicative null model for combined effects given a log link). Macroalgal percent cover was modelled using a beta distribution with a logit link, suitable for proportional, bounded (0−1) data (see Supplementary Methods (Analyses) for details on model choices). Barnacle and macroalgal models supported full random-effect structures (site-level variation in intercepts and full slope structure), whereas grazer models with full random-slope structures produced singular fits. A full AIC/singularity grid search showed that the enrichment-only random slope (alongside random intercepts) was the best supported non-singular specification, indicating relatively homogeneous between-site variation in warming and interaction responses that do not support random slopes, compared with the more heterogeneous enrichment response across sites (see Supplementary Methods (Analyses) for details). Fixed effects were interpreted on the transformed scale and back-transformed for reporting. For log-linked models, we exponentiated coefficients ($\exp(\beta)$ = multiplicative change; percent change = $(\exp(\beta) - 1) \times 100$). For the beta-logit model, we converted predicted log-odds to proportions via the inverse-logit, multiplying by 100 to obtain percent cover. Final specifications and diagnostics are provided in SI Table S2. We assessed warming × enrichment interactions on each functional group model's link scale relative to an additive null expectation (i.e. additivity on the link scale), and used a predefined ±5% equivalence band around the null to distinguish negligible from more notable departures relative to the null model. Full definitions and interaction classification rules are provided in the Supplementary Methods (Analyses).

To quantify site deviations from global effects, we extracted model BLUPs (best linear unbiased predictions (Haslett & Puntanen, 2017; Robinson, 1991): shrinkage-aware site-specific random effects) with accompanying conditional variances (summarised as Wald 95% CIs) and added them to the fixed effects to obtain per-site treatment effects on the model's

link scale. For barnacles and macroalgae, all BLUPs were back-transformed for interpretation, reported as percent changes for barnacles (multiplicative scale) and as odds ratios and/or expected proportions for macroalgae (logit scale) (see Supplementary Methods (Analyses) for further details). For grazers, random warming/interaction slopes were not supported, so we derived empirical within-site log-scale contrasts for those terms, propagating the within-site standard errors of the log-mean treatment values to obtain Wald 95% CIs, and present these alongside BLUP-based nutrient enrichment slopes. Across all response groups, we report site effects as both percent changes to convey proportional responses given different site-level baselines, as well as on the link-scale. Finally, we used the resulting per-site effects for exploratory biogeographic comparisons, applying Welch's t-tests to compare effects across temperate vs. non-temperate sites, and Pearson correlations with absolute latitude. Full supplementary tables and figures are provided in SI Tables S9 and S10, and SI Fig. S2.

Meta-regressions

We ran two complementary sets of meta-regressions to explain variability across locations in sensitivity to each stressor. Site-specific stressor effects were derived from the fitted GLMMs on each model's link scale, and then back-transformed for interpretability (percentage change in means (log); percentage change in odds (logit)). To limit statistical multiplicity, we pre-specified a small, mechanistic moderator set, and, except where the moderator was itself experimental, evaluated moderators in a single baseline stratum (to avoid underpowered three-way tests). Across all responses and moderators, this yielded 30 tests. We report two-sided *p*-values and emphasise effect sizes, CIs/precision, sign consistency, and sensitivity checks; associations should thus be interpreted qualitatively. Full details are provided in the Supplementary Methods (Analyses).

Warming sensitivity asked whether sites that experienced larger absolute heating (ΔWarming, °C) showed systematically stronger warming effects. ΔWarming was computed as the seasonal difference in mean daily maximum plate temperatures between warmed and ambient plates at each site (see Fig. 2). We treat ΔWarming as absolute °C because thermal physiology depends strongly on absolute temperature thresholds and rate laws, making degree-based effects mechanistically interpretable (Buckley et al., 2001; Kobayashi et al., 2014). For each response group, we first derived a site-specific warming effect from the fitted GLMM, then related that effect to ΔWarming. For barnacle abundance and macroalgal

cover, the warming contrast under non-enriched plates was the model's fixed effect for warming plus the site random slope; under nutrient-enriched plates we added the Warming × Enrichment term (fixed + site random effect) to obtain the contrast between nutrient enrichment conditions. For grazers, where random warming slopes were not supported, we computed the same two contrasts empirically from site-level cell means on the log scale (non-enriched: log(mean(warm)) − log(mean(ambient)); enriched: same plus the interaction contrast). Each site-specific warming contrast (on the link scale) was then back-transformed as appropriate (percentage change in the mean for log-Gaussian models; percentage change in odds for the beta-logit model). We related these effect sizes to ΔWarming using simple OLS fits (unweighted given small *n*), reporting r, slope, and two-sided *p*-values. Because ΔWarming is an experimental moderator, we analysed its association with the warming response separately for enriched and non-enriched sites. All other warming moderators (biogeographic and local context) were evaluated in the non-enriched baseline only to isolate modifiers of warming without complication of co-occurring nutrient effects. For warming, we considered: 1) climate zone (temperate vs. non-temperate); 2) absolute latitude; and 3) mechanistic thermal descriptors, including mean daily maximum temperature and SD of daily temperature range, both chosen to capture thermal forcing and extreme-heat exposure expected to mediate losses under warming.

Nutrient enrichment sensitivity asked whether sites with stronger enrichment showed larger enrichment effects, with enrichment expressed as response ratios of enriched vs. non-enriched nitrate measured over the same period (see Methods and Fig. 2). In contrast to warming, nutrient pulses are experienced relative to background conditions (osmoregulation/toxicity scale with enrichment over baseline), so response ratios best reflect ecological dose and enable comparability across innately oligotrophic to eutrophic regimes (Martínez-García et al., 2012; Noe et al., 2001; Ponce-Soto et al., 2015). For each site, we extracted the enrichment effect from the GLMM (fixed term + site random slope; adding the interaction term to obtain the effect under warmed plates for the stratified analysis) and back-transformed it to percent change for barnacle and grazer abundance (log links) or percent change in odds for macroalgal cover (logit). For the meta-regressions, we quantified nitrate enrichment as a log response ratio, $\ln RNO_3 = \ln(E / NE)$, where R is the enrichment ratio (E / NE) comparing the summer mean at the enriched shore (E) to its paired non-enriched shore (NE). This is based on the same site-level means used for the descriptive proportional elevation summaries, but here we take the natural log of the enrichment ratio.

Taking the natural log of this ratio makes multiplicative effects additive and symmetric (for example, a doubling, R = 2, and a halving, R = 0.5, become +ln2 and −ln2), reduces skew and heteroskedasticity, and makes regression slopes easier to interpret per one-unit change in lnR. Sites where NE ≈ 0 (requiring a pseudo-count in descriptive summaries) were excluded from lnR-based regressions to avoid leverage from near-zero denominators; consequently, Portugal (Porto) was omitted from nitrate-based meta-regressions (see Methods and Supplementary Methods (Experimental)). These site-specific enrichment effects were then related to $lnRNO_3$ using simple OLS regressions, analysed separately for ambient and warmed plates. All other enrichment moderators (hydrometeorological and catchment) were evaluated under ambient thermal conditions only, for interpretability and power, as with the warming meta-regressions. For comparability across sites, we focused on nitrate, as it was measured consistently across locations and is often the proximate limiting nutrient in coastal marine waters, strongly implicated in eutrophication impacts (Howarth & Marino, 2006; Paerl, 2018). Hydrometeorological and catchment moderators were limited to mean daily precipitation (mm/day) and human-dominated land cover (%) within 5 km (definition and processing in Supplementary Methods (Experimental); maps in SI Fig. S1). We did not include latitude or climate zone here because the focus is local enrichment relative to local background rather than broad biogeography, and omitting non-causal predictors helps constrain statistical multiplicity. These variables capture variation in both the delivery and source strength of nutrient inputs: wetter catchments are expected to experience more frequent and intense runoff and effluent pulses, while more human-dominated land cover may reflect greater point and diffuse nutrient sources.

Structural equation modelling (SEM)

We fitted a piecewise SEM to recover mechanistic networks by which stressors affect these communities, estimating direct and indirect pathways simultaneously. As with the GLMMs, we analysed summer-averaged plate responses per treatment within each site. Warming and nutrient enrichment were treated as exogenous drivers, and biotic groups were endogenous responses linked by a priori pathways based on competitive and trophic interactions. Full SEM details are provided in the Supplementary Methods (Analyses).

The *a priori network* encoded three expectations: 1) warming depresses macroalgal cover and barnacle abundance via thermal/desiccation stress (Harley et al., 2006; Helmuth & Hofmann, 2001); 2) nutrient enrichment increases macroalgal cover and phytoplankton, potentially

elevating invertebrate abundances (Kraufvelin, 2007; Kraufvelin et al., 2002); 3) macroalgal cover suppresses barnacle abundance via space competition and may facilitate grazers via food/refuge (Bertness & Leonard, 1997; Bruno et al., 2003). We fit one mixed model per endogenous node on appropriate transformed scales: macroalgal cover as logit (proportion cover); barnacle and grazer abundance as log(count + 1), using Gaussian distributions after diagnostics (and for compatibility with piecewise SEM, see Supplementary Methods (Analyses)). Warming and enrichment entered the macroalgae and barnacle sub-models as fixed effects. The grazer sub-model included enrichment and macroalgae only, with no a priori direct warming path given likely behavioural buffering by mobile grazers. We specified a directed negative macroalgae → barnacles path and a directed positive macroalgae → grazers path. All sub-models included a random intercept for site. We also allowed a site-specific random slope for nutrient enrichment to accommodate heterogeneity among sites, while holding warming slopes common to avoid over-parameterisation and singular fits. Because barnacles were absent across Argentine replicates and macroalgal cover was negligible on Chilean plates, each respective sub-model used its appropriate data; piecewise SEM estimates equations locally, so unequal sample sizes across components are valid (Lefcheck, 2016). We additionally ran a common-site sensitivity by refitting reduced sub-models on the intersection of sites and found the direction and significance of the core paths (warming → macroalgal cover; warming → barnacle abundance; macroalgal cover → barnacle abundance) unchanged. We therefore retain the per-sub-model filtering in the primary SEM and report the common-site sensitivity as a robustness check in the Supplementary Methods (Analyses).

We began with the full *a priori* SEM, including interaction terms in the macroalgae and barnacle sub-models, and removed unsupported interactions to retain parsimony without altering the sign of core paths. D-separation tests flagged an independence violation caused by mixing macroalgae scales across equations; we therefore harmonised macroalgal cover to the logit scale in all sub-models. We also compared two representations of macroalgae–barnacle competition, a directed negative path versus a residual covariance, and retained the supported directed path. Finally, d-separation suggested a residual association between barnacle and grazer abundances consistent with a shared, unmeasured driver. Adding a post-hoc residual covariance (Barnacles %~~% Grazers; Fig. 6) improved global fit without changing the sign or significance of core paths.

We report standardised path coefficients obtained by z-scoring each variable on its model scale to facilitate comparison across paths; unstandardised coefficients are provided in SI Table S3. Indirect mediated effects were quantified via parametric bootstrap (1,000 resamples): at each draw we refit sub-models, rebuilt the SEM, recomputed direct/indirect effects, and summarised 95% percentile CIs. We interpret indirect effects as supported when their CI excludes zero. Global fit was evaluated with Shipley's d-separation/Fisher's C.

4.5 Supplementary information

4.5.1 Supplementary methods (experimental)

Initial collaborator recruitment

We assembled our collaborative network of global installations through an open call posted on social media (LinkedIn and X, formerly Twitter), followed by targeted emails to fill geographic gaps. Interested teams were screened against practical inclusion criteria: 1) access to paired and clearly differentiated nutrient-enriched and non-enriched rocky shorelines within each location; 2) capacity to install experimental plates appropriately at mid-intertidal height; and 3) commitment to the installation and sampling schedule, and associated *in situ* measurements. Where multiple groups expressed interest in the same region, we prioritised locations that maximised biogeographic spread across climate zones. We also weighed feasibility of permitting, logistics, and costs. We prioritised sites where *in situ* installations were permissible without extensive bureaucratic approval processes, and where local teams could directly cover most material costs; where that was not possible, we partially reallocated funds to maintain geographic coverage. Some regions could not be included due to an inability to secure installation permits or due to financial limitations (most notably continental Africa). A small number of sites were lost post-deployment due to plate detachment, removal, or loss of access (e.g. one Vietnam site and one Peru site), resulting in the final set of 11 paired locations (22 sites). A full list of principal site characteristics is provided in Table 1.

Site midpoint and climate classification procedure

We used the V2 global Köppen–Geiger climate classification map for 1991–2020 published by Beck et al. (2023) at 0.01° (~1 km) resolution. The GeoTIFF was read into R via the raster package and reclassified so that each integer code (1−30) could be mapped to its corresponding climate class. Site midpoints (i.e. between each nutrient-enriched and non-enriched site) were computed geodesically from the paired site coordinate pairs using geosphere, converted to an sf object, and snapped to the nearest land cell on a global coastline layer (from rnaturalearth) to ensure points fell on land rather than ocean. Using raster::extract, the Köppen–Geiger code was retrieved directly for each midpoint. In cases where a midpoint landed over a NoData cell, we applied a 10 km radius buffer around the

point and took the modal climate code to assign the most representative adjacent land climate.

Notably, for Ushuaia (Argentina), the snapped coastal midpoint returned ET (tundra) in the Beck et al. (2023) 1991–2020 (0.01°) Köppen–Geiger V2 map. Southern Patagonia/Tierra del Fuego is widely described as a transition zone where subpolar oceanic (Cfc) and tundra (ET) conditions occur in close proximity (Bujalesky, 2007; Xia et al., 2020). The C/E boundary in Köppen–Geiger is defined by the ~10 °C warmest-month threshold (temperate 'C' requires ≥ 1 month with mean temperature > 10 °C; polar 'E/ET' has warmest month < 10 °C); small coastal/gridded differences near that threshold can flip a pixel between Cfc and ET (Beck et al., 2023; Peel et al., 2007). Beck et al. (2023) also report subclass accuracy ~79−86% (depending on period) and explicitly note that pinpointing a single class is more challenging near transition boundaries and under the influence of coastal microclimates, particularly in recent decades (Beck et al., 2023). Accordingly, we retain ET as the extracted Köppen–Geiger class for our Ushuaia midpoint. However for binary 'Temperate/Non-temperate' groupings used in subsequent analyses (Temperate = all C classes; Non-temperate = all other classes), Ushuaia is treated as 'Temperate' (ET/Cfc transition) as it lies within the documented South American temperate forest belt (≈ 33–55° S) and the Magellanic/Subpolar forest region around Magallanes and Tierra del Fuego where cool-temperate *Nothofagus* forests persist, consistent with an ocean-moderated, forested sub-Antarctic setting rather than being analogous with a polar tundra classification (D'Antoni et al., 2007; Donoso et al., 2022).

Plate design

Intertidal ectotherms often track substratum rather than air temperatures because heat transfer is dominated by conduction, not convection; warming the substrate therefore provides a biologically relevant thermal cue (Denny & Harley, 2006; Kordas et al., 2015, 2017; Kordas & Harley, 2016; LaScala-Gruenewald & Denny, 2020). We implemented this by deploying black (warmed) and white (ambient) settlement plates constructed from HDPE sheet. Each plate carried a central patch of marine-grade epoxy that served as the settlement surface. To maximise durability, we mechanically abraded the HDPE contact area before epoxy application; early pilots without this step resulted in partial or full delamination after several weeks. The epoxy layer (PC-11 Marine, off-white) was spread to ~2–3 mm thickness

and textured while curing using rock salt that was later dissolved, producing a heterogeneous surface for community settlement.

Plate design was inspired by previous studies on intertidal warming (Kordas et al., 2015, 2017; Kordas & Harley, 2016), with modifications to ensure scalability and robustness. First, we used thinner HDPE surface panels (2 cm thickness) to reduce weight and shipping costs while retaining stiffness adequate for handling and wave exposure. Second, all fasteners and exposed fittings were stainless steel to minimise corrosion and staining in marine environments. Third, to monitor the thermal manipulation directly at the substrate, we embedded ElectricBlue EnvLogger T2.4 temperature loggers in a router-cut recess on the plate underside, positioning the logger in direct contact with the underside of the epoxy patch. The EnvLogger units were selected for marine tolerance, battery life, and cost efficiency for multi-site deployments (procured on a batch basis), and were configured to log at the same interval network-wide (90 min; see Methods). Across sites, this design delivered a consistent elevation of the warmed substrate (mean maximum ≈ +1.4 °C relative to white controls; see main text Fig. 1C), while maintaining identical geometry and surface area between treatments so that colour-driven thermal absorption was the only systematic, categorical difference. Site-specific elevations in ADM (average of daily maxima; i.e. the mean of daily maximum plate temperatures over the sampling window) and Max (maximum plate temperature recorded over the sampling window) during the sampling period are shown in Fig. 2.

Nutrient enrichment verification

For installation, we operationally defined nutrient-enriched and non-enriched shorelines at each location based on local expert knowledge of persistent nutrient sources (e.g. wastewater outfalls, marinas, aquaculture, river mouths) and/or a rapid pre-installation spot check, recognising that such pre-checks were not feasible everywhere due to variable access to probes, laboratory facilities, and budgets. Formal nutrient verification was conducted during the experimental summer only: at each sampling visit, collaborators obtained paired water samples from the nutrient-enriched and non-enriched areas and quantified nitrate (NO_3^-) and phosphate (PO_4^{3-}). Methods reflected local capacity: some teams used portable in situ probes, while others collected bottled samples for laboratory analysis (standard colourimetric assays or equivalent), with calibration/controls performed according to local protocols. All readings were harmonised to common units prior to analysis (mg/L). Importantly, every

sampling visit included paired nutrient measurements, ensuring that the nutrient-enriched/non-enriched designation was empirically checked throughout the season, even when pre-installation spot checks were unavailable.

Importantly, while for our study the categorical site contrasts are defined by nutrient concentrations, we recognise that they occur within broader coastal pollution regimes (e.g. organic matter, contaminants associated with wastewater or runoff), and our enrichment treatment therefore represents a realistic composite of nutrient loading and co-occurring pollutants rather than nutrients in isolation.

Quantifying nutrient enrichment and summaries

For each location and nutrient (NO_3^-; PO_4^{3-}), we first averaged all replicate measurements within each nutrient condition (enriched, non-enriched) over the experimental summer to obtain site-level mean concentrations (mg/L). Let NE and E denote the non-enriched and enriched summer means, respectively. Because some non-enriched sites were extremely oligotrophic (NE ≈ 0), directly forming a simple ratio E/NE can yield arbitrarily large values and strongly distort cross-site summaries.

To stabilise the denominator at very low background concentrations, we defined a small, nutrient-specific pseudo-count ε and used a capped non-enriched mean NE* = max(NE, ε) when computing proportional enrichment. ε was estimated separately for NO_3^- and PO_4^{3-} as:

- [$\varepsilon = \max(0.0001\ \text{mg/L}, 0.05 \times q_{0.05})$],

where $q_{0.05}$ is the 5th percentile of non-zero non-enriched means for that nutrient across all sites. This yields very small floors ($\varepsilon(NO_3^-) \approx 0.00085$ mg/L; $\varepsilon(PO_4^{3-}) \approx 0.00026$ mg/L), which only affect sites where NE is effectively zero. In practice, ε was triggered only for one nitrate site (Porto, Portugal); all other sites had NE > ε and therefore used their observed non-enriched mean. We then expressed enrichment as percent change:

- Percent enrichment = [$100 \times (E - NE) / NE^*$],

where NE* is the non-enriched mean defined above, as the larger of either the site NE mean, or ε. This formulation converts fold-changes to proportional differences, while avoiding divide-by-zero artefacts at ultra-oligotrophic sites.

For cross-site summaries, the main text reports the mean ± 1 SE of percentage enrichment across locations after excluding ε-triggered sites (Porto, Portugal), to prevent a single site with NE ≈ 0 from dominating the global average (Fig. 1E and 2). Here, SE was computed as SD/√n across locations (i.e. variation across sites, not within-site temporal variability). On this basis, the mean global proportional enrichment was approximately +615% for NO_3^- and +312% for PO_4^{3-}. To complement the mean, we also summarise the distribution of proportional enrichment across sites via robust median [IQR]: NO_3^- = +184% [111–306%] and PO_4^{3-} = +102% [94–292%]. Finally, Fig. 2 presents all site-specific percent enrichments for both nutrients as a heat map, with the colour scale capped at the 90th percentile of non-ε sites for readability; each tile is labelled with the exact percent enrichment, and tiles where NE ≤ ε (i.e. ε was used) are marked accordingly.

Sampling schedule

Installation schedules were constrained by delays in international shipping and permitting, which compressed the planned establishment window (target ≈ 7 months) to 5–6 months at some locations. To ensure viable communities despite this compression, local coordinators made site-specific decisions based on knowledge of settlement windows and turnover rates (e.g. rapid barnacle and grazer recruitment on warm coasts), proceeding only where establishment was expected to be sufficient for the method (ultimately, no location received materials with < 5 months of *in situ* acclimation time before the first sampling date). We then sampled during each location's summer window, when plate warming is maximised, following the mid-tide installation standard used across locations. Our intended frequency was fortnightly (8 visits); several locations achieved all eight, many achieved 7–8, and a minority completed fewer visits due to tides, weather, staffing, or access interruptions. To avoid uneven time-series weightings and to emphasise the seasonal response, we aggregated to a summer mean per plate per treatment (with no imputation). This approach: 1) treats each location's season as the unit of inference; 2) is robust to irregular intervals, cases where plate detachments created uneven replicate numbers (only notable in the Madeira location, where all but one ambient plate was lost in the non-enriched site), and occasional missed visits due to logistical constraints, and 3) aligns with the wider SEM/GLMM framework,

where inference is defined on plate-level, season-average responses rather than short-term dynamics.

CountThings model specification

To standardise barnacle abundance counts across locations and sampling dates, we used the CountThings mobile app workflow to analyse overhead photographs taken within the 40% stencil window to avoid edge effects (see Methods). The model is based on convolutional neural-network object detection and was fine-tuned on our own annotated images collected during the acclimation period and early sampling. Training images deliberately spanned multiple barnacle morphologies (e.g. *Semibalanus*, *Chthamalus*-type forms), sizes (new recruits to adults), lighting conditions, epibiont cover, and epoxy textures, so that the detector would generalise across locations and image qualities. An additional label was used to distinguish live individuals (intact opercula visible) from dead individuals (opercula absent). We applied a single decision threshold across the project to balance precision and recall, and maintained quality-control measures: 1) plates with very low densities (≤ 10 individuals) were counted in situ by eye rather than by model; and 2) images showing prohibitive motion blur, glare, or water droplets were entered as NA in the data frame and excluded. Model performance used standard metrics: precision, recall, F1 score, mean average precision (mAP), intersection-over-union (IoU), average precision per class, average recall, and false-positive rate. Detailed architecture, training/augmentation options, and deployment settings are proprietary to CountThings (www.countthings.com). Limitations to note are potential under-counting of very small recruits at the resolution limit, and occasional misclassification under heavy turf or sediment, both mitigated by manual review when feasible.

ImageJ colour thresholding

We quantified macroalgal cover (%) from overhead images of the entire epoxy settlement area using ImageJ. For each plate, we first defined the region of interest (ROI) as the epoxy surface with the rectangle tool and cropped to the ROI to avoid edge artefacts. Colour thresholding was then performed with Color Threshold in the RGB colour space, using the default threshold method and red overlay for visual feedback. As a starting template, we applied narrow green-biased bounds (R: 0–50; G: 0–255; B: 0–50) to maximise macroalgal pigments and suppress barnacle/epoxy hues; thresholds were then tuned slightly per location to accommodate differences in illumination, sensor white balance, and local algal chroma, ensuring full bounding of algal cover. Selected pixels were converted to a black-and-white

binary mask, and Area Fraction was measured. Because the mask renders selected algae as black and background as white, we report % cover = 100 − Area Fraction.

Weather data processing

To derive extreme-event metrics in a site- and season-specific way, we computed thresholds from the respective daily series, defining a heatwave threshold as mean(tempmax) + sd(tempmax) and a cold-snap threshold as mean(tempmin) − sd(tempmin). We then identified runs of ≥ 3 consecutive days above (sustained heat) or below (cold snap) those thresholds. We also defined heavy rain as days exceeding the 90th percentile of that site's daily precipitation; gust extremes as days above the 90th percentile of daily peak wind gust; high UV as days with UV index ≥ 8 (with runs again defined as ≥ 3 days); sunny days as those with cloud cover < 20%; fog days as visibility < 1 km; and dry-spell length as the longest consecutive run of precipitation = 0. The variable dictionary below (Table S1) distinguishes downloaded daily variables (summarised to seasonal means or totals) from derived variability, cumulative, and extreme-event metrics.

Land use data processing

We quantified land use around each location using the ESA CCI Land Cover 2022 product (C3S-LC-L4-LCCS-Map-300 m-P1Y-2022-v2.1.1), extracting the categorical band lccs_class. Following the official LCCS legend, we defined human-dominated land as cropland (classes 10–40) plus urban/built-up (class 190). Pixels coded as permanent or coastal water (classes 210 and 220) were masked to NA so that human cover percentages were computed over land only. Within each 5 km buffer, we computed the percentage of human-dominated land by first counting the number of land pixels (i.e. non-NA after water masking) and then counting pixels whose class belonged to cropland or urban categories. The final metric for each location was calculated as (human_pixels / land_pixels) × 100 and stored as pct_human_landcover_5km.

To visually validate classifications, we produced small panel maps for each location (Fig. S1). For these plots, land-cover classes were grouped into six intuitive categories: (1) Cropland (10–40), (2) Urban (190), (3) Forest (50, 60, 70, 100, 110), (4) Shrub/grassland (121, 130, 140, 150), (5) Sparse/barren (160, 170), and (6) Other (all remaining terrestrial classes), all rendered within the 5 km circle, with the site centre and buffer boundary overlaid. Notably, the 300 m spatial resolution of the product can under-resolve narrow coastal features and

mixed shoreline pixels; masking water before computing percentages helps to avoid inflating the denominator with ocean cells. In addition, the 5 km radius was chosen a priori as a pragmatic balance between the immediate shoreline context of our experimental method and the likely influence of nearby catchments.

4.5.2 Supplementary methods (analyses)

GLMMs

For barnacles, count data were aggregated to plate means, then modelled as continuous log-transformed responses using a Gaussian LMM of log(AvgBarnacles + 1). To ensure our log-Gaussian model was not disproportionately influenced by the choice of small constant added to zero counts, we performed a sensitivity analysis across a range of plausible pseudo-counts. Specifically, we refit the mixed model using offsets of 0.1, half the minimum non-zero plate mean (0.125), 0.25, 0.30, 0.40, …, and 1.0, each time extracting the fixed-effect estimates, *p*-values, and AIC. Across every offset, the warming coefficient reliably sat near −0.60 on the log scale (≈45% decline), the nutrient enrichment coefficient around +0.34 (≈40% increase), and the Warming × Enrichment interaction near −0.15 (≈15% damping), with the latter two always far from statistical significance (all $p > 0.49$). While larger offsets tended to reduce AIC slightly, the overall inferential pattern held uniformly. Second, we re-ran the model using an inverse hyperbolic sine transform (asinh) instead of log(y + k) to handle zeros without any added constant; this specification yielded nearly identical fixed effects, *p*-values, and qualitative interpretations, but with a higher AIC (650.7 vs. 595.8). We therefore adopt the conventional log(AvgBarnacles + 1) transformation for consistency with the broader ecological literature, noting that our key conclusions about warming's suppressive effect, and the lack of a robust nutrient enrichment or interaction effect, remain unchanged under both conservative and permissive pseudo-count choices and alternative zero-handling strategies.

A similar workflow was followed for grazer abundance, with aggregation and sensitivity analysis of the log constant. Given zeros/near-zeros, this outperformed alternatives (e.g. Gamma) and produced the best AIC/fit among candidate families. Notably, we ran an explicit AIC/singularity search over random-slope sets, with the enrichment-only random slope (plus random intercepts) best supported and producing a non-singular fit (AIC ≈ 415). Any attempt to also include warming or interaction slopes produced singular fits; interaction-only and intercept-only variants had substantially higher AIC values.

Macroalgal cover was expressed as a continuous proportion between 0 and 1 at the plate-level (percent cover / 100). We modelled this response using a beta regression with a logit link (glmmTMB), which is well suited to strictly bounded proportional data where variance typically changes with the mean. Because the beta family requires responses strictly within (0, 1), proportions were clipped using a small epsilon (0.001) to avoid exact 0/1 values. To improve numerical stability for the full random-slope structure, the beta-logit model was fit with glmmTMBControl (optimiser = optim, optArgs = list(method = "BFGS"), profile = TRUE), yielding a positive-definite Hessian and successful convergence. DHARMa residual checks on this final optimiser-stabilised model showed no evidence of misfit (no significant departures from uniformity, dispersion, zero-inflation, or outliers). Alternative beta variants fit without the optimiser (and related alternatives, e.g. cloglog/zero-inflation) showed convergence/Hessian problems, so the optimiser-stabilised beta-logit model was retained as the primary GLMM. All coefficients are estimated on the logit scale and back-transformed to predicted proportions (and hence percent cover) for reporting in the main text.

Models were fitted in R using lme4 (Gaussian LMMs) and glmmTMB (beta-logit), with DHARMa diagnostics; per-site effects were derived as BLUPs (random effects + fixed effects) on the link scale and back-transformed for interpretation. A summary of the final GLMM model specifications and brief notes on rationale can be found in Table S2.

We classified the effect of interactions on the model link scale using a two-stage rule. First, we form a null expectation ($\Delta add = \beta warm + \beta enrich$), i.e. the prediction if there were no non-linear interaction. The joint/observed effect on the link scale is represented as $\Delta joint = \beta warm + \beta enrich + \beta int = \Delta add + \beta int$; thus, βint is the deviation from the additive prediction ($\Delta joint - \Delta add$). On multiplicative links (log, multiplicative on the mean; or logit, multiplicative on the odds scale), we summarised deviation via the interaction ratio ($\exp(\beta int)$) and applied a ±5% equivalence band around 1 (0.95–1.05), whereby this margin indicates only mild deviation from the null model. Similarly, on identity-scale models we used a ±5% band around the null prediction on the raw scale ($\pm 0.05 \times (\alpha + \Delta add)$). This framing follows standard equivalence-testing logic, whereby an upper and lower bound is specified based on a smallest effect size of interest (SESOI) (Lakens, 2017), used here to separate negligible from more notable departures relative to the null model. Only when the interaction term was statistically significant were interactions labelled as non-linearities; even then, we considered them negligible/mild when the CI lay within the predefined equivalence band for

qualitative interpretation. When significant, synergism indicates the interaction reinforces the net effect predicted by adding the single-stressor effects, pushing the response further in that same direction; whereas antagonism dampens it by pulling the response back toward the null expectation. When main effects oppose each other, synergism is an interaction that shares the sign of the additive expectation (reinforces), and antagonism has the opposite sign (counteracts). Furthermore, we flag potential reversals, whereby the interaction flips the overall sign of the predicted response (i.e. Δjoint has a different sign than Δadd). Where the interaction term is statistically insignificant, the interaction term remains unclassified.

Meta-regressions

For the warming meta-regression, plate heating during emersion is governed by radiative loading and convective cooling, while splash/immersion provides thermal relief. We therefore selected moderators that capture peak exposure and thermal volatility, rather than distal climatology:

- Mean daily maximum temperature: represents the central tendency of the hottest part of each day, when organisms are most likely to approach or exceed critical thermal and desiccation thresholds. If responses are driven by short high-temperature windows, sites with higher daily maxima may show steeper warming sensitivities.
- SD of daily temperature range: indexes day-to-day variability in diel heating/cooling, capturing thermal volatility and the frequency/magnitude of rapid shifts. Fluctuating thermal regimes can alter performance even when mean temperatures are similar (via non-linear thermal performance curves and exceedance dynamics), and can also create mismatches between recent thermal history and the next day's peak if acclimation lags behind variability.

For the enrichment meta-regression, because coastal nutrient inputs are strongly delivery- and retention-limited, we prioritised hydrology and catchment context over broad geography:

- % human-dominated land cover (cropland + urban): proxy for chronic nutrient source pressure (fertiliser, effluent, impervious surfaces).
- Mean precipitation: proxy for runoff/effluent pulsing and hydrological delivery (with potential dilution effects).

- *We do not include latitude/climate zone here because the ecological dose of enrichment is set locally by source pressure and hydrology; adding non-causal geographic context increases multiplicity without supporting mechanistic insights.*

In both meta-analyses, we regressed the GLMM-derived site effect against its matching local moderator using Pearson correlations and unweighted OLS trend lines with 95% CI bands. For each stressor, we first estimated the association in a predefined baseline condition and then repeated the same association separately under the alternative level of the other stressor. Specifically, warming effects were related to moderators first using non-enriched sites only, and then repeated for nutrient-enriched sites; nutrient-enrichment effects were similarly related to moderators first using ambient plates only, and then repeated for warmed plates. For warming, we additionally compared temperate vs. non-temperate sites with Welch's t-tests and correlated effects with absolute latitude and thermal descriptors. For nutrient enrichment, we examined hydrometeorological and catchment moderators, and did not include latitude or climate zone by design. All analyses were unweighted, univariable, and treated two-sided *p*-values as descriptive; we did not propagate GLMM uncertainty into weights, fit multi-moderator models, adjust for multiple testing, or run formal influence diagnostics. Given the modest number of sites, results are presented as pattern-finding summaries rather than formal, fully specified meta-analytic models. Accordingly, these results are intended to contextualise between-site patterns and guide interpretation of the GLMM effects, rather than replace them.

Because Vietnam had substantially higher mean precipitation than all other sites, we evaluated whether the significant precipitation-response relationships were driven by this single site. We repeated the ambient-condition single-moderator models as leave-one-out analyses and as a reduced dataset excluding Vietnam. For barnacle abundance, the positive association with mean precipitation weakened and lost nominal significance when Vietnam was removed ($r = 0.46$, $p = 0.254$). For grazer abundance, the strong precipitation signal likewise became non-significant when Vietnam was excluded ($r = 0.53$, $p = 0.144$). Influence diagnostics confirmed Vietnam as a high-leverage point with large Cook's distances in both grazer and barnacle precipitation models, indicating disproportionate influence on slope estimates (SI Table S13B). We therefore report single-moderator results including all sites but interpret their strength and generality with caution, noting that directionality is consistently positive, whereas precision and significance depend strongly on Vietnam.

SEM

All three sub-models were fitted as Gaussian mixed models on transformed responses so they could be combined in a piecewise SEM. Macroalgal cover was analysed on the logit scale after converting percent cover to proportions and clipping to (0, 1) to accommodate boundary values. Barnacle abundance and grazer abundance were analysed on the log(count + 1) scale. Accordingly, the piecewiseSEM output reports the component models as "gaussian/identity", reflecting linear mixed-model fits on transformed responses; coefficients should be interpreted on the relevant transformed scale unless explicitly back-transformed.

We began with the a priori network and removed unsupported stressor interactions for parsimony, yielding a reduced SEM. Relative to the full specification, the reduced model had similar AIC but substantially improved global d-separation fit, although it still showed lack of fit (Full: AIC = 1664.00, Fisher's C = 331.64, df = 10, $p \approx 3.13 \times 10^{-65}$; Reduced: AIC = 1669.29, Fisher's C = 19.98, df = 4, $p \approx 5.05 \times 10^{-4}$). We therefore treat this reduced specification as the baseline structure, and the covariance-augmented model (below) as the primary SEM used for inference and figures. Raw and standardised path coefficients (with *p*-values) are reported in Table S3, and marginal/conditional R^2 per node are reported in Table S4. Because d-separation for the reduced SEM suggested a residual association between barnacle abundance and grazer abundance (consistent with shared, unmodelled drivers), we evaluated a post-hoc residual covariance between these nodes. Adding this covariance improved global fit (Fisher's C = 4.14, df = 2, $p = 0.126$) without altering the directed path estimates; the standardised residual covariance was −0.120 ($p \approx 0.026$), interpretable as a residual correlation on the z-scaled metric. We report this as a sensitivity (it improves absolute fit but does not add directed structure), and provide the associated d-separation claims in Table S5 (see also Table S14A, residual-covariance row).

We also evaluated additional variants. Dropping site-level random slopes for nutrient enrichment (random intercepts only) worsened fit (AIC = 1985.10, Fisher's C = 80.37, $p \approx 1.45 \times 10^{-16}$), supporting retention of site-specific enrichment slopes. Representing macroalgal cover → barnacle abundance competition as a residual covariance (rather than a directed path) reduced explanatory power (AIC = 1698.27, Fisher's C remained poor), so we retained the directed pathway for interpretability and fit. Because piecewise SEM estimates

each sub-model locally, we used per-sub-model filtering where required by response absence (macroalgal cover negligible in Chile; barnacles absent in Argentina). To confirm this did not drive inference, we refit the reduced SEM on the intersection of sites shared by all three sub-models (per-sub-model filtering: Fisher's C = 19.98, df = 4, $p \approx 5.05 \times 10^{-4}$; common-site intersection: Fisher's C = 17.71, df = 4, p ≈ 0.001). Importantly, the core path signs and significance were consistent, so we retain the per-sub-model SEM as primary and report the common-site refit as a robustness check. Finally, we tested adding a direct warming → grazer abundance path; d-separation did not reject the implied conditional independence of warming and grazers given other predictors, and adding the path did not improve inference, so we omitted it from the primary SEM.

4.5.3 Supplementary tables

Methods

Category	Name (data column name)	Unit	Definition/ computation	Source
Seasonal means (raw daily variables)	mean_daily_max_temp	°C	Mean of daily maximum air temperature.	Downloaded -> mean
	mean_daily_min_temp	°C	Mean of daily minimum air temperature.	
	mean_daily_temp	°C	Mean of daily mean air temperature.	
	mean_humidity	%	Mean daily relative humidity.	
	mean_daily_precip	mm	Mean daily precipitation amount.	
	mean_windgust	m s^{-1}	Mean of daily peak wind gust.	
	mean_daily_windspeed	m s^{-1}	Mean of daily windspeed.	
	mean_sealevelpressure	hPa	Mean sea-level pressure.	
	mean_cloudcover	%	Mean daily cloud cover.	
	mean_visibility	km	Mean daily horizontal visibility.	
	mean_solarradiation	W m^{-2}	Mean daily incoming shortwave radiation.	
	mean_solarenergy	Wh m^{-2}	Mean daily total shortwave energy.	
	mean_uvindex	index	Mean of daily maximum UV index.	
Variability/range	mean_temp_range	°C	Mean of daily diurnal temperature range.	Derived
	sd_temp_range	°C	Std. dev. of daily diurnal temperature range.	
	sd_precip	mm	Std. dev. of daily precipitation.	
	sd_windspeed	m s^{-1}	Std. dev. of daily windspeed.	
	sd_sealevelpressure	hPa	Std. dev. of daily sea-level pressure.	
Cumulative	total_precip	mm	Sum of seasonal daily precipitation.	
	total_solar_energy	Wh m^{-2}	Sum of seasonal daily solar energy.	
Extremes: counts and runs	heatwave_runs	count	Number of ≥3-day heatwave runs.	
	heatwave_days	days	Total days within heatwave runs.	
	cold_snap_runs	count	Number of ≥3-day cold snap runs.	
	cold_snap_days	days	Total days within cold snap runs.	
	heavy_rain_days	days	Days with precipitation above site 90th percentile.	
	dry_spell_max	days	Longest consecutive run with precipitation = 0.	
	gust_extreme_days	days	Days with wind gust peak above site 90th percentile.	
	sunny_days	days	Days with cloud coverage <20%.	
	high_UV_runs	count	Number of ≥3-day runs with UV index ≥8.	
	high_UV_days	days	Total days with UV index ≥8.	
	fog_days	days	Days with visibility <1km.	

Table S1 | Weather metrics dictionary. Complete downloaded and derived site-season summaries at each geodesic midpoint for variables used in context analyses (note: only a subset was used in analyses; see Methods). "Downloaded → mean/sum" are seasonal means or totals of daily fields; "Derived" metrics quantify variability and extremes. "Runs" count ≥3 consecutive days; "days" totals all days meeting the threshold. Units follow conventions of Visual Crossing.

Response	Family/link (fit scale)	Response transformation	Fixed effects	Random effects	Notes
Barnacle abundance	Gaussian (log scale)	log(AvgBarnacles + 1)	• Warming • Enrichment • Warming × Enrichment	• Intercept • Full random slopes	Log(+1) constant chosen following sensitivity analysis; qualitative outputs stable across offsets. Asinh gave similar inference but slightly higher AIC; log(+1) retained for interpretability and consistency with literature.
Grazer abundance	Gaussian (log scale)	log(AvgGrazers + 1)	• Warming • Enrichment • Warming × Enrichment	• Intercept • Enrichment slope (best non-singular approach)	Log(+1) constant chosen in same way to barnacle GLMM. Enrichment-only slope retained by grid search, whereby all other combinations resulted in singular fits.
Macroalgal cover	Beta (logit)	Proportion (0–1)	• Warming • Enrichment • Warming × Enrichment	• Intercept • Full random slopes	Beta-logit appropriate for bounded proportions; ε-clipping avoids 0/1. Final model fit with optim(method="BFGS") + profile=TRUE for stability of full random-slope structure (pdHess TRUE; convergence 0); DHARMa checks on final model showed no evidence of misfit.

Table S2 | Summary of final GLMM specifications and selection rationale.

Outcome	Predictor	Raw (Estimate)	Std. error	df	Crit. value	Standardised (z)	p-value
logit_algae	Warming	−0.417	0.119	190.5	−3.50	−0.100	<0.001
logit_algae	Enrichment	0.719	0.393	21.7	1.83	0.173	0.0660
log_AvgBarnacles	Warming	−0.909	0.090	190.4	−10.05	−0.238	<0.001
log_AvgBarnacles	Enrichment	0.490	0.509	21.0	0.96	0.128	0.337
log_AvgBarnacles	logit_algae	−0.330	0.094	240.0	−3.50	−0.358	<0.001
log_AvgGrazers	logit_algae	−0.005	0.040	196.3	−0.17	−0.011	0.869
log_AvgGrazers	Enrichment	0.391	0.319	21.4	1.23	0.208	0.226

Table S3 | Directed path coefficients for primary reduced SEM (no interactions, per-sub-model filtering, random intercepts by site and a random slope for enrichment by site). Columns report the raw estimates on each sub-model's link scale (Estimate; logit for macroalgae, log(count + 1) for barnacles and grazers), their standard errors, Satterthwaite DF, test statistic, standardised (z-scaled) effects, and p-values.

Outcome	Marginal R^2	Conditional R^2
logit_algae	0.07	0.70
log_AvgBarnacles	0.19	0.86
log_AvgGrazers	0.04	0.78

Table S4 | Marginal R^2 (fixed effects only) and conditional R^2 (fixed + random effects) for each endogenous node (macroalgae, barnacles, grazers) from the primary reduced SEM. Values are computed on the fitted model scales.

Independence claim (given the model)	Test type	df	Crit. value	p-value
log_AvgGrazers ~ Warming | (Enrichment, Algae)	coef	236.9	−1.53	0.127
log_AvgGrazers ~ log_AvgBarnacles | (Warming, Enrichment, Algae)	coef	192.2	3.63	<0.001 (i.e. support post-hoc residual covariance)

Table S5 | Key d-separation claims motivating subsequent sensitivity analyses. Directed separation (conditional independence) tests that 1) justified omission of a warming → grazer abundance path, and 2) flagged residual barnacle–grazer association, modelled post-hoc as a covariance.

Results

Response	Term	Estimate (link)	SE	p-value	Back-transformed	95% CI (back-transformed)	% change	95% CI (% change)
Barnacle abundance	Warming	−0.608	0.201	0.082	0.544	[0.249, 1.188]	−45.6	[-75.1, 18.8]
	Enrichment	0.335	0.466	0.490	1.398	[0.489, 3.995]	39.8	[-51.1, 299.5]
	Interaction	−0.148	0.233	0.548	0.863	[0.492, 1.513]	−13.7	[-50.8, 51.3]
Grazer abundance	Warming	−0.146	0.082	0.075	0.864	[0.735, 1.015]	−13.6	[-26.5, 1.5]
	Enrichment	0.322	0.295	0.297	1.380	[0.725, 2.625]	38.0	[-27.5, 162.5]
	Interaction	0.123	0.114	0.282	1.131	[0.903, 1.415]	13.1	[-9.7, 41.5]
Macroalgal cover	Warming	−0.388	0.145	0.007	0.678	[0.511, 0.901]	−32.2	[-48.9, -9.9]
	Enrichment	0.502	0.289	0.082	1.653	[0.937, 2.914]	65.3	[-6.3, 191.4]
	Interaction	0.103	0.189	0.587	1.108	[0.765, 1.604]	10.8	[-23.5, 60.4]

Table S6 | Summary of fixed-effect estimates from the generalised linear mixed models (GLMMs). Barnacle abundance and grazer abundance were analysed using Gaussian mixed models fit to log-transformed plate-mean abundances (log(mean + 1)); macroalgal cover was analysed using a beta regression with a logit link on proportional cover (0–1). For each response, the table reports the fixed-effect estimate, standard error, and two-sided p-value on the model's link scale (identity for log-Gaussian; logit for beta). Back-transformed effects are reported as multiplicative change in mean abundance (barnacles/grazers; exp(β)) or odds ratios (macroalgal cover), with 95% CIs and the corresponding percent change defined as (ratio − 1) × 100.

Response	Stressor	Baseline context	Ratio	95% CI	% change	95% CI (% change)	p-value
Barnacle abundance	Warming	Non-enriched	0.544	[0.328, 0.904]	−45.6	[−67.2, −9.6]	0.021
		Enriched	0.470	[0.307, 0.719]	−53.0	[−69.3, −28.1]	0.002
	Enrichment	Ambient	1.398	[0.479, 4.083]	39.8	[−52.1, 308.3]	0.503
		Warmed	1.206	[0.402, 3.621]	20.6	[−59.8, 262.1]	0.715
Grazer abundance	Warming	Non-enriched	0.864	[0.735, 1.016]	−13.6	[−26.5, 1.6]	0.077
		Enriched	0.977	[0.835, 1.142]	−2.3	[−16.5, 14.2]	0.768
	Enrichment	Ambient	1.380	[0.708, 2.688]	38.0	[−29.2, 168.8]	0.317
		Warmed	1.560	[0.801, 3.037]	56.0	[−19.9, 203.7]	0.173
Macroalgal cover	Warming	Non-enriched	0.678	[0.511, 0.901]	−32.2	[−48.9, -9.9]	0.007
		Enriched	0.752	[0.557, 1.014]	−24.8	[−44.3, 1.4]	0.062
	Enrichment	Ambient	1.653	[0.937, 2.914]	65.3	[−6.3, 191.4]	0.082
		Warmed	1.831	[1.031, 3.252]	83.1	[3.1, 225.2]	0.039

Table S7 | Pairwise contrasts of estimated marginal means (EMMs) for each response. 'Warming' contrasts warmed vs. ambient within each nutrient context; 'Enrichment' contrasts nutrient-enriched vs. non-enriched within each warming level. Ratios and 95% CIs are on the back-transformed scale (barnacle and grazer abundance: multiplicative change in mean; macroalgal cover: odds ratios). Percent change is defined as (ratio − 1) × 100 (percent change in odds for macroalgal cover). Two-sided p-values are from GLMM contrast tests on the model scale.

Response	Intercept SD	Warming SD	Enrichment SD	Interaction SD
Barnacle abundance	1.61	0.49	1.42	0.48
Grazer abundance	0.55	NA	0.94	NA
Macroalgal cover	0.99	0.17	0.81	0.12

Table S8 | Standard deviations of site-level random effects around the global fixed effects. Values are standard deviations of random-effect terms estimated on each model's link scale (barnacle and grazer abundance: log-transformed Gaussian scale; macroalgal cover: logit). 'NA' indicates the final model did not include that random slope.

Site	Term	Link estimate (log)	SE	95% CI (link)	% change
Chile	Warming	−0.940	0.270	[−1.469, −0.412]	−60.9
	Enrichment	−0.660	0.321	[−1.289, −0.031]	−48.3
	Interaction	0.070	0.357	[−0.629, 0.769]	7.3
Denmark	Warming	−0.795	0.270	[−1.324, −0.267]	−54.9
	Enrichment	2.326	0.321	[1.697, 2.955]	923.9
	Interaction	−0.239	0.357	[−0.939, 0.460]	−21.3
Ecuador	Warming	−0.442	0.270	[−0.971, 0.086]	−35.7
	Enrichment	−0.568	0.321	[−1.197, 0.061]	−43.3
	Interaction	0.211	0.357	[−0.488, 0.911]	23.5
Greenland	Warming	−0.586	0.270	[−1.115, −0.058]	−44.4
	Enrichment	0.557	0.321	[−0.072, 1.186]	74.6
	Interaction	−0.248	0.357	[−0.947, 0.451]	−22.0
Norway	Warming	−0.571	0.270	[−1.099, −0.042]	−43.5
	Enrichment	−0.207	0.321	[−0.836, 0.422]	−18.7
	Interaction	−0.652	0.357	[−1.351, 0.047]	−47.9
New Zealand	Warming	−0.603	0.270	[−1.131, −0.074]	−45.3
	Enrichment	−0.770	0.321	[−1.399, −0.141]	−53.7
	Interaction	0.219	0.357	[−0.480, 0.918]	24.5
Portugal 1 (Madeira)	Warming	0.417	0.336	[−0.241, 1.075]	51.7
	Enrichment	−1.569	0.437	[−2.426, −0.713]	−79.2
	Interaction	−0.596	0.401	[−1.382, 0.190]	−44.9
Portugal 2 (Porto)	Warming	−1.109	0.270	[−1.637, −0.580]	−67.0
	Enrichment	−0.308	0.321	[−0.937, 0.321]	−26.5
	Interaction	−0.001	0.357	[−0.700, 0.698]	−0.1
UK	Warming	−0.961	0.270	[−1.489, −0.432]	−61.7
	Enrichment	2.156	0.321	[1.527, 2.785]	763.8
	Interaction	0.147	0.357	[−0.552, 0.846]	15.9
Vietnam	Warming	−0.493	0.270	[−1.022, 0.035]	−38.9
	Enrichment	2.394	0.321	[1.765, 3.023]	996.0
	Interaction	−0.386	0.357	[−1.085, 0.313]	−32.0

Table S9A | Barnacle site-level effects. Best linear unbiased predictions (BLUPs) of site-specific treatment effects for warming, nutrient enrichment, and their interaction from the barnacle model (Gaussian mixed model on log(mean abundance + 1)). Shown are site-level estimates on the model scale, their model-based standard errors and Wald 95% CIs derived from the conditional random-effect variance, and the corresponding back-transformed percent changes.

Site	Term	Source	Link estimate (log)	SE	95% CI (link)	% change
Argentina	Warming	Empirical	−0.267	0.287	[−0.829, 0.295]	−23.4
	Enrichment	BLUP	−0.370	0.181	[−0.725, −0.016]	−31.0
	Interaction	Empirical	0.433	0.390	[−0.330, 1.197]	54.2
Chile	Warming	Empirical	0.113	0.457	[−0.782, 1.007]	11.9
	Enrichment	BLUP	−0.577	0.181	[−0.932, −0.223]	−43.9
	Interaction	Empirical	0.324	0.634	[−0.918, 1.566]	38.3
Denmark	Warming	Empirical	−0.303	0.116	[−0.531, −0.075]	−26.1
	Enrichment	BLUP	1.094	0.181	[0.740, 1.449]	198.7
	Interaction	Empirical	−0.190	0.706	[−1.574, 1.193]	−17.3
Ecuador	Warming	Empirical	0.002	0.100	[−0.195, 0.199]	0.2
	Enrichment	BLUP	−0.311	0.181	[−0.665, 0.044]	−26.7
	Interaction	Empirical	−0.134	0.262	[−0.647, 0.379]	−12.6
Greenland	Warming	Empirical	0.062	0.057	[−0.051, 0.174]	6.3
	Enrichment	BLUP	−0.431	0.181	[−0.786, −0.077]	−35.0
	Interaction	Empirical	−0.084	0.062	[−0.205, 0.037]	−8.0
New Zealand	Warming	Empirical	0.000	0.071	[−0.138, 0.138]	0.0
	Enrichment	BLUP	−0.478	0.181	[−0.833, −0.124]	−38.0
	Interaction	Empirical	0.037	0.080	[−0.119, 0.194]	3.8
Norway	Warming	Empirical	−0.185	0.225	[−0.626, 0.256]	-16.9
	Enrichment	BLUP	−0.527	0.181	[−0.881, −0.172]	−41.0
	Interaction	Empirical	0.016	0.427	[−0.820, 0.853]	1.6
Portugal 1 (Madeira)	Warming	Empirical	−0.693	0.000	[−0.693, −0.693]	-50.0
	Enrichment	BLUP	−0.576	0.228	[−1.022, −0.129]	−43.8
	Interaction	Empirical	0.693	0.000	[0.693, 0.693]	100.0
Portugal 2 (Porto)	Warming	Empirical	−0.481	0.317	[−1.103, 0.140]	−38.2
	Enrichment	BLUP	−0.708	0.181	[−1.062, −0.353]	−50.7
	Interaction	Empirical	0.404	0.387	[−0.354, 1.162]	49.8
UK	Warming	Empirical	−0.112	0.088	[−0.285, 0.061]	−10.6
	Enrichment	BLUP	0.467	0.181	[0.113, 0.822]	59.6
	Interaction	Empirical	0.100	0.134	[−0.163, 0.363]	10.6
Vietnam	Warming	Empirical	−0.133	0.177	[−0.480, 0.215]	−12.4
	Enrichment	BLUP	2.417	0.181	[2.062, 2.771]	1020.8
	Interaction	Empirical	0.139	0.225	[−0.303, 0.581]	14.9

Table S9B | Grazer site-level treatment effects. Warming and interaction terms are empirical log-scale contrasts computed from site-level treatment means (random slopes for these terms were not supported by the final Gaussian LMM). Their standard errors and 95% CIs are approximate Wald intervals obtained by propagating within-site uncertainty in the log-mean treatment values. Nutrient enrichment effects are site-level BLUP-based nutrient-enrichment slopes on the model (log) scale (global fixed effect + site deviations), with standard errors and 95% CIs derived from the conditional random-effect variance. Percent change is the corresponding back-transformed percentage change in grazer abundance relative to the relevant reference treatment. Where a treatment cell is based on very low replication (e.g. Portugal 1 warming/interaction), propagated uncertainty can be effectively zero and the CIs collapse to the point estimate.

Site	Term	Link estimate (logit)	SE	95% CI (link)	% change (odds)
Argentina	Warming	−0.230	0.207	[−0.635, 0.175]	−20.5
	Enrichment	0.593	0.401	[−0.193, 1.380]	81.0
	Interaction	0.267	0.284	[−0.290, 0.823]	30.6
Denmark	Warming	−0.272	0.121	[−0.509, −0.036]	−23.8
	Enrichment	0.138	0.375	[−0.597, 0.874]	14.9
	Interaction	0.167	0.129	[−0.085, 0.419]	18.2
Ecuador	Warming	−0.408	0.210	[−0.821, 0.004]	−33.5
	Enrichment	−0.366	0.370	[−1.092, 0.360]	−30.7
	Interaction	−0.028	0.243	[−0.505, 0.449]	−2.8
Greenland	Warming	−0.385	0.061	[−0.504, −0.267]	−32.0
	Enrichment	0.509	0.354	[−0.184, 1.202]	66.3
	Interaction	0.106	0.046	[0.016, 0.196]	11.2
Norway	Warming	−0.325	0.116	[−0.553, −0.097]	−27.7
	Enrichment	−0.090	0.358	[−0.792, 0.611]	−8.6
	Interaction	0.087	0.092	[−0.093, 0.268]	9.1
New Zealand	Warming	−0.660	0.357	[−1.360, 0.039]	−48.3
	Enrichment	2.547	0.406	[1.752, 3.342]	1176.7
	Interaction	0.103	0.270	[−0.427, 0.634]	10.9
Portugal 1 (Madeira)	Warming	-0.598	0.214	[−1.017, −0.178]	−45.0
	Enrichment	0.863	0.418	[0.043, 1.682]	137.0
	Interaction	−0.052	0.270	[−0.582, 0.477]	−5.1

Portugal 2 (Porto)	Warming	−0.375	0.091	[−0.553, −0.198]	−31.3
	Enrichment	0.170	0.356	[−0.528, 0.867]	18.5
	Interaction	0.073	0.080	[−0.083, 0.229]	7.5
UK	Warming	−0.112	0.291	[−0.683, 0.459]	−10.6
	Enrichment	0.199	0.459	[−0.700, 1.099]	22.1
	Interaction	0.329	0.388	[−0.431, 1.088]	38.9
Vietnam	Warming	−0.526	0.184	[−0.886, −0.166]	−40.9
	Enrichment	0.400	0.369	[−0.322, 1.123]	49.2
	Interaction	−0.043	0.248	[−0.529, 0.444]	−4.2

Table S9C | Macroalgal site-level effects. Site-specific treatment BLUPs from the beta-regression model (logit link). Estimates, standard errors, and Wald 95% CIs are on the logit scale, obtained from the conditional random-effect variance; percent change is reported as percent change in odds after back-transformation.

Response	Term	Mean temperate	Mean non-temperate	Difference (temperate − non-temperate)	t-value	df	p-value
Barnacle abundance	Warming	-39.6	-41.2	1.6	0.10	6.4	0.922
	Enrichment	353.7	4.2	349.5	1.78	6.4	0.122
	Interaction	-7.2	-15.4	8.2	0.36	2.9	0.746
Grazer abundance	Warming	-18.6	-3.5	-15.1	-1.52	6.4	0.176
	Enrichment	134.0	-34.2	168.2	1.29	7.0	0.238
	Interaction	31.8	-6.3	38.1	2.79	8.2	0.023
Macroalgal cover	Warming	-31.5	-31.1	-0.4	-0.08	7.1	0.941
	Enrichment	214.2	9.0	205.2	1.25	6.4	0.255
	Interaction	13.8	5.9	8.0	1.04	7.8	0.328

Table S10A | Comparison of site-level effects between temperate and non-temperate zones. Values are group means (percent change for barnacle and grazer abundance; percent change in odds for macroalgal cover) and their difference (temperate − non-temperate). p-values are from two-sided Welch two-sample t-tests (allowing unequal variances).

Response	Term	r-value	p-value (r)	Slope (% per °lat)	95% CI (slope)	R^2
Barnacle abundance	Warming	−0.258	0.473	−0.43	[−1.74, 0.88]	0.067
	Enrichment	0.023	0.951	0.50	[−17.52, 18.51]	0.001
	Interaction	−0.369	0.294	−0.50	[−1.52, 0.52]	0.136
Grazer abundance	Warming	−0.044	0.898	−0.04	[−0.77, 0.68]	0.002
	Enrichment	−0.322	0.334	−5.20	[−16.70, 6.31]	0.104
	Interaction	−0.083	0.808	−0.15	[−1.51, 1.21]	0.007
Macroalgal cover	Warming	0.436	0.208	0.24	[−0.16, 0.65]	0.19
	Enrichment	−0.015	0.968	−0.26	[−14.48, 13.96]	0.000
	Interaction	0.580	0.079	0.41	[−0.06, 0.87]	0.336

Table S10B | Association between site-level effects and absolute latitude. r and its p-value are from Pearson correlation; slope and 95% CIs are from an ordinary least-squares (OLS) regression of effect on absolute latitude; R^2 is from the same OLS model. Effects are expressed as percent change for barnacle and grazer abundance and percent change in odds for macroalgal cover.

Response	Nutrient context	r-value	95% CI (r)	p-value	Slope	95% CI (slope)
Barnacle abundance	Non-enriched	−0.034	[−0.650, 0.609]	0.926	−1.38	[−34.81, 32.05]
	Enriched	−0.574	[−0.884, 0.087]	0.083	−13.61	[−29.45, 2.23]
Grazer abundance	Non-enriched	−0.303	[−0.764, 0.363]	0.366	−7.33	[−24.74, 10.08]
	Enriched	−0.307	[−0.766, 0.359]	0.358	−9.02	[−30.08, 12.04]
Macroalgal cover	Non-enriched	0.544	[−0.130, 0.874]	0.104	7.55	[−1.94, 17.04]
	Enriched	0.452	[−0.248, 0.842]	0.189	12.47	[−7.58, 32.53]

Table S11A | Warming meta-regression: relating ΔWarming (°C; warmed − ambient mean daily maximum plate temperature) to the site-level warming effect, estimated separately for non-enriched and nutrient-enriched sites. Reported are Pearson correlations (r, 95% CI, p) and OLS slopes with 95% CIs. Effects are expressed as percent change in mean abundance (barnacles, grazers) or percent change in odds of macroalgal cover; slopes therefore quantify change in that effect metric per +1 °C.

Response	r-value	95% CI (r)	p-value	Slope	95% CI (slope)
Barnacle abundance	−0.258	[−0.763, 0.444]	0.473	−0.43	[−1.74, 0.88]
Grazer abundance	−0.044	[−0.627, 0.571]	0.898	−0.04	[−0.77, 0.68]
Macroalgal cover	0.436	[−0.267, 0.836]	0.208	0.24	[−0.16, 0.65]

Table S11B | Warming meta-regression: associating absolute latitude (°) with the warming effect estimated from non-enriched sites only. Reported are Pearson correlations (r, 95% CI, p) and OLS slopes with 95% CIs. Effects are expressed as percent change in mean abundance (barnacles, grazers) or percent change in odds of macroalgal cover.

Response	Temperate mean	Non-temperate mean	Difference (temperate − non-temperate)	95% CI (diff)	t-value	df	p-value
Barnacle abundance	−39.6	−41.2	+1.6	[−36.8, 40.0]	0.10	6.4	0.922
Grazer abundance	−18.6	−3.5	−15.1	[−39.1, 8.9]	−1.52	6.4	0.176
Macroalgal cover	−31.5	−31.1	−0.4	[−13.5, 12.7]	−0.08	7.1	0.941

Table S11C | Warming meta-regression: comparison of the warming effect between temperate and non-temperate sites, using effects estimated from non-enriched sites only. Reported are group means, the difference in % change of response groups between temperate and non-temperate sites (temperate - non-temperate) with 95% CIs, t, df, and two-sided p-values from Welch two-sample t-tests. Effects are expressed as percent change in mean abundance (barnacles, grazers) or percent change in odds of macroalgal cover.

Response	Moderator	r-value	95% CI (r)	p-value	Slope	95% CI (slope)
Barnacle abundance	Mean daily max (°C)	0.254	[−0.447, 0.762]	0.479	1.25	[−2.63, 5.14]
	SD of daily range (°C)	−0.668	[−0.914, −0.067]	0.035	−25.46	[−48.56, -2.35]
Grazer abundance	Mean daily max (°C)	−0.178	[−0.703, 0.473]	0.601	−0.48	[−2.48, 1.52]
	SD of daily range (°C)	0.184	[−0.468, 0.706]	0.589	4.13	[−12.54, 20.81]
Macroalgal cover	Mean daily max (°C)	−0.379	[−0.814, 0.329]	0.280	−0.59	[−1.76, 0.58]
	SD of daily range (°C)	0.466	[−0.231, 0.847]	0.174	6.76	[−3.69, 17.21]

Table S11D | Warming meta-regression: associations of the warming effect with continuous thermal moderators (mean daily maximum temperature; SD of daily temperature range), using effects estimated from non-enriched sites only. Reported are Pearson correlations (r, 95% CI, p) and OLS slopes with 95% CIs. Effects are expressed as percent change in mean abundance (barnacles, grazers) or percent change in odds of macroalgal cover.

Response	Thermal context	r-value	95% CI (r)	p-value	Slope	95% CI (slope)
Barnacle abundance	Ambient	−0.230	[−0.776, 0.512]	0.551	−108.17	[−516.66, 300.33]
	Warmed	−0.295	[−0.802, 0.459]	0.441	−118.91	[−463.41, 225.58]
Grazer abundance	Ambient	0.054	[−0.596, 0.661]	0.882	26.24	[−367.64, 422.11]
	Warmed	0.054	[−0.596, 0.661]	0.882	29.67	[−417.96, 477.29]
Macroalgal cover	Ambient	0.004	[−0.662, 0.666]	0.992	1.47	[−348.31, 351.26]
	Warmed	−0.037	[−0.684, 0.643]	0.925	−15.94	[−403.15, 371.28]

Table S12A | Nutrient-enrichment meta-regression: nitrate response ratio ($lnRNO_3$ = ln(E / NE)) versus the site-level nutrient-enrichment effect, estimated separately for ambient and warmed plates. Reported are Pearson correlations (r, 95% CI, p) and OLS slopes with 95% CIs. Effects are expressed as percent change in mean abundance (barnacles, grazers) or percent change in odds of macroalgal cover; slopes therefore quantify change in that effect metric per +1 unit of $lnRNO_3$. A +1 unit increase corresponds to multiplying nitrate by e ≈ 2.72.

Response	Moderator	r-value	95% CI (r)	p-value	Slope	95% CI (slope)
Barnacle abundance	Human land cover (%)	0.083	[−0.615, 0.708]	0.831	1.41	[−13.62, 16.43]
	Mean precipitation (mm/day)	0.641	[−0.040, 0.915]	0.063	65.59	[−4.63, 135.81]
Grazer abundance	Human land cover (%)	−0.069	[−0.670, 0.586]	0.850	−1.20	[−15.27, 12.88]
	Mean precipitation (mm/day)	0.977	[0.902, 0.995]	<0.001	102.94	[84.57, 121.32]
Macroalgal cover	Human land cover (%)	0.172	[−0.513, 0.723]	0.635	2.21	[−8.12, 12.54]
	Mean precipitation (mm/day)	−0.168	[−0.721, 0.516]	0.643	−13.74	[−79.61, 52.16]

Table S12B | Nutrient-enrichment meta-regression: associations of the nutrient-enrichment effect with hydrometeorological and catchment moderators, using effects estimated from ambient plates only. Reported are Pearson correlations (r, 95% CI, p) and OLS slopes with 95% CIs. Slope units: % human land cover = change in effect metric per +1% cover; mean precipitation = change in effect metric per +1 mm/day. Effects are expressed as percent change in mean abundance (barnacles, grazers) or percent change in odds of macroalgal cover.

Response	Moderator	Set	r-value	95% CI (r)	p-value	N	Slope	95% CI (slope)
Barnacle abundance	Mean precipitation (mm/day)	All sites	0.641	[−0.040, 0.915]	0.063	9	65.59	[−4.62, 135.81]
		No Vietnam	0.457	[−0.365, 0.879]	0.254	8	182.54	[−171.98, 537.05]
Grazer abundance	Mean precipitation (mm/day)	All sites	0.977	[0.902, 0.995]	<0.001	10	102.94	[84.57, 121.32]
		No Vietnam	0.528	[−0.210, 0.882]	0.144	9	61.24	[−26.89, 149.36]

Table S13A | Sensitivity of the mean-precipitation moderator to excluding Vietnam (ambient warming treatment). Pearson correlations (r, 95% CI, p, N) and OLS slopes (95% CI) are reported with and without Vietnam. Note: N differs across response groups irrespective of Vietnam exclusion because some sites lacked the focal biotic group (see main text). Only barnacle and grazer abundance are shown because no moderators were significant for macroalgal cover.

Response	Model	Site	Leverage (hat)	Cook's D
Barnacle abundance	Enrichment effect ~ mean precipitation	Vietnam	0.961	8.769
Grazer abundance	Enrichment effect ~ mean precipitation	Vietnam	0.960	15.287

Table S13B | Influence diagnostics for Vietnam. For each model, we report per-site leverage (hat value) and Cook's distance. We define a large Cook's distance using the common threshold > 4/n, where n is the number of sites in that model (e.g. barnacles: n = 9 → 4/n ≈ 0.44; grazers: n = 10 → 4/n ≈ 0.40). High leverage indicates extreme predictor values; high leverage coupled with large Cook's D indicates disproportionate influence on the fitted slope.

Outcome	Predictor	Path	Point estimate (95% CI)	Total (95% CI)	p (direct)
Barnacle abundance (log[abundance + 1])	Enrichment	Direct	0.128 [−0.143, 0.428]	0.128 [−0.143, 0.428]	0.337
	Warming	Direct	−0.238 [−0.373, −0.190]	−0.238 [−0.373, −0.190]	<0.001
	Macroalgal cover (logit)	Direct	−0.358 [−0.579, −0.257]	−0.358 [−0.579, −0.257]	<0.001
	Enrichment	Indirect (Enrichment → Macroalgal cover → Barnacles)	−0.062 [−0.156, −0.004]	0.066 [−0.220, 0.356]	NA
	Warming	Indirect (Warming → Macroalgal cover → Barnacles)	0.036 [0.015, 0.073]	−0.202 [−0.335, −0.157]	NA
Grazer abundance (log[abundance + 1])	Enrichment	Direct	0.208 [−0.110, 0.492]	0.208 [−0.110, 0.492]	0.226
	Macroalgal cover (logit)	Direct	−0.011 [−0.161, 0.123]	−0.011 [−0.161, 0.123]	0.869
	Enrichment	Indirect (Enrichment → Macroalgal cover → Grazers)	−0.002 [−0.036, 0.025]	0.206 [−0.109, 0.476]	NA
	Warming	Indirect (Warming → Macroalgal cover → Grazers)	0.001 [−0.012, 0.018]	0.001 [−0.012, 0.018]	NA
Macroalgal cover (logit)	Enrichment	Direct	0.173 [0.010, 0.334]	0.173 [0.010, 0.334]	0.0660
	Warming	Direct	−0.100 [−0.161, −0.043]	−0.100 [−0.161, −0.043]	<0.001
Residual covariance	NA	Barnacles ~~ Grazers	−0.122	−0.122	0.0260

Table S14A | Standardised coefficients (z-scored) of the piecewise SEM. Point estimate is the path coefficient. Total is the sum of the direct effect and all indirect effects connecting the same predictor–response pair via the listed mediator pathway. 95% CIs are bootstrap intervals from the piecewise SEM (NA for the residual covariance). The p (direct only) column reports the model p-value for the direct edge only (Welch/Satterthwaite tests from the component sub-models); indirect rows do not have p-values.

Outcome	Predictor	Path	Point estimate (95% CI)	Total (95% CI)	p (direct)
Barnacle abundance (log[abundance + 1])	Enrichment	Direct	0.490 [−0.473, 1.458]	0.490 [−0.473, 1.458]	0.337
	Warming	Direct	−0.909 [−1.070, -0.735]	−0.909 [−1.070, −0.735]	<0.001
	Macroalgal cover (logit)	Direct	−0.330 [−0.429, −0.225]	−0.330 [−0.429, −0.225]	<0.001
	Enrichment	Indirect (Enrichment → Macroalgal cover → Barnacles)	−0.237 [−0.506, -0.014]	0.253 [−0.706, 1.241]	NA
	Warming	Indirect (Warming → Macroalgal cover → Barnacles)	0.138 [0.049, 0.228]	−0.771 [−0.958, −0.581]	NA
Grazer abundance (log[abundance + 1])	Enrichment	Direct	0.391 [−0.192, 0.979]	0.391 [−0.192, 0.979]	0.226
	Macroalgal cover (logit)	Direct	−0.005 [−0.067, 0.055]	−0.005 [−0.067, 0.055]	0.869
	Enrichment	Indirect (Enrichment → Macroalgal cover → Grazers)	−0.004 [−0.067, 0.046]	0.388 [-0.197, 0.962]	NA
	Warming	Indirect (Warming → Macroalgal cover → Grazers)	0.002 [−0.024, 0.032]	0.002 [−0.024, 0.032]	NA
Macroalgal cover (logit)	Enrichment	Direct	0.719 [0.041, 1.390]	0.719 [0.041, 1.390]	0.0660
	Warming	Direct	−0.417 [−0.669, −0.178]	−0.417 [−0.669, −0.178]	<0.001

Table S14B | Raw model-scale coefficients of the piecewise SEM component sub-models. Macroalgal cover is on the logit scale; barnacle abundance and grazer abundance are on the log(abundance + 1) scale. Reported metrics match Table S14A (point estimate; total effect where applicable; bootstrap 95% CIs; and p-values for direct edges only).

4.5.4 Supplementary figures

Methods

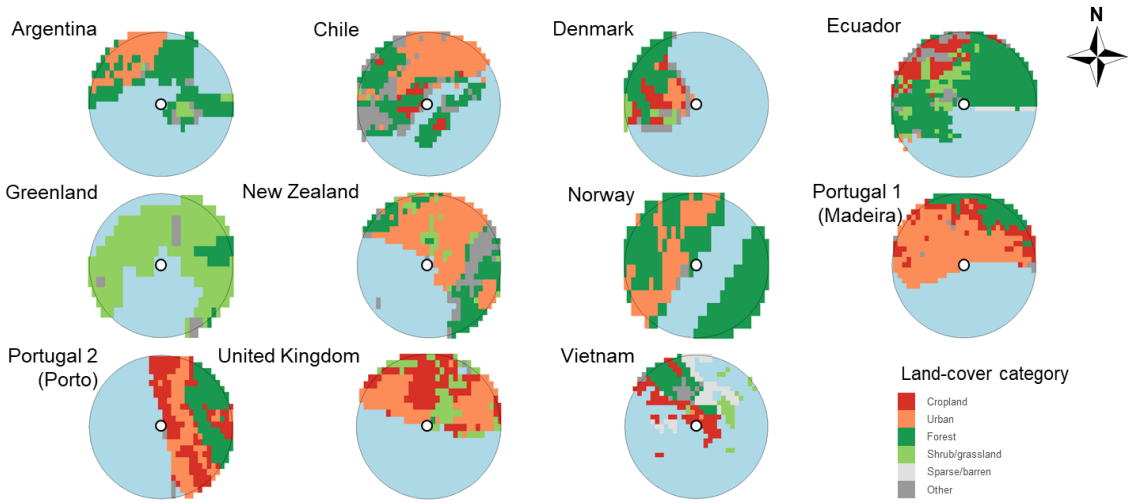


Figure S1 | Land cover context around each site midpoint (5 km radius). Panels show categorical land cover from the ESA CCI Land Cover 2022 product (300 m; band lccs_class) aggregated into six classes: Cropland (classes 10–40), Urban/built-up (190), Forest (50, 60, 70, 100, 110), Shrub/grassland (121, 130, 140, 150), Sparse/barren (160, 170), and Other (all remaining terrestrial classes). Permanent/coastal water (210, 220) is masked so percentages are computed over land only. The open dot marks the site midpoint; the circle is the 5 km buffer used for calculations. These maps were used to visually quality control the % human-dominated land cover (cropland + urban) used in analyses.

Results

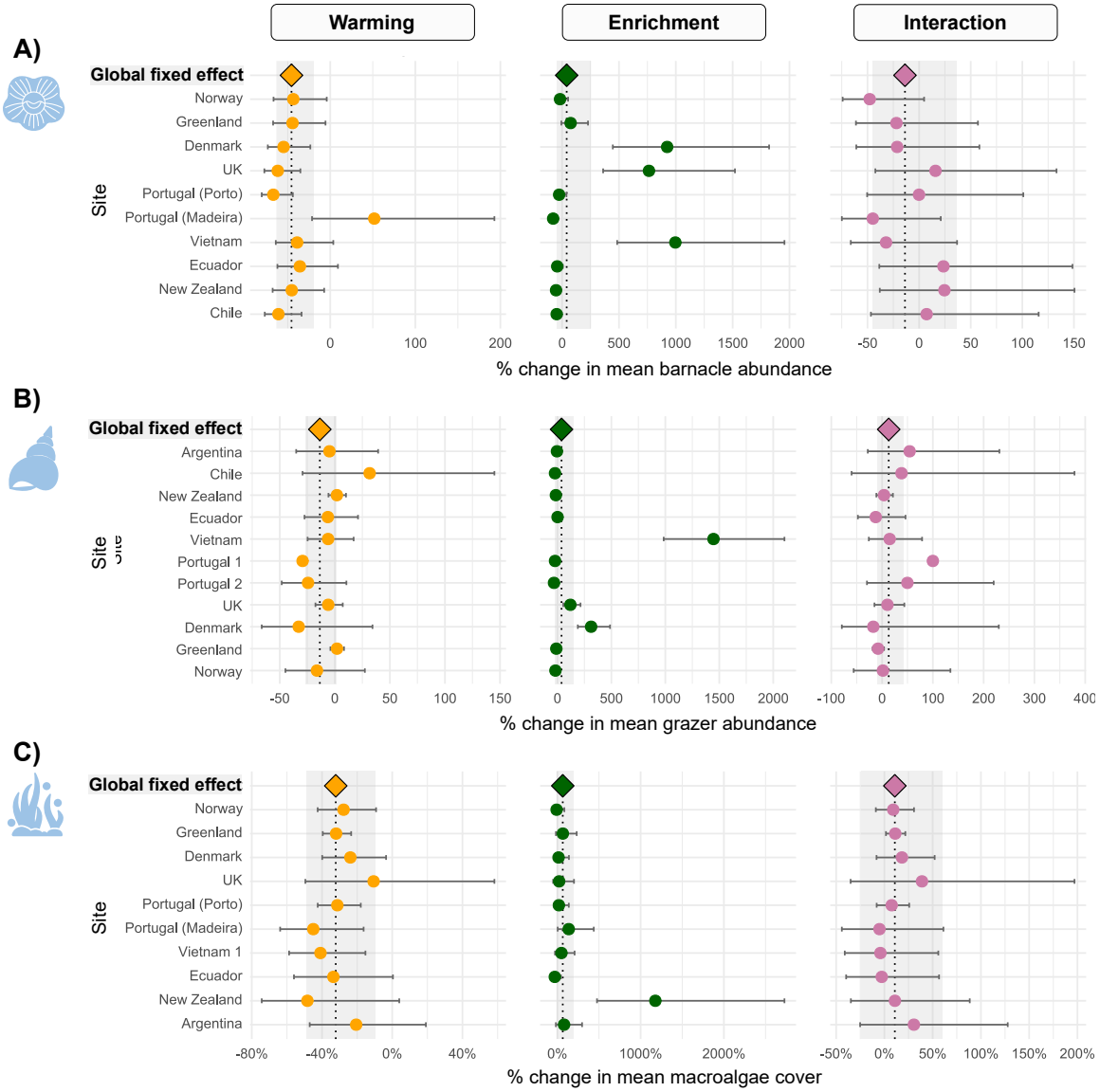


Figure S2 | Back-transformed site-level treatment effects. Points show per-site treatment effects (fixed effects plus site-specific deviations) back-transformed to percent change. Panels show: A) percent change in mean barnacle abundance; B) percent change in mean grazer abundance; and C) percent change in odds of macroalgal cover. Dashed vertical lines indicate the global fixed-effect estimates; grey shaded vertical ribbons show their 95% CIs from the mixed models. Horizontal bars show uncertainty around site effects. For barnacle abundance and macroalgal cover, uncertainty intervals are model-based Wald 95% CIs derived from the conditional random-effect variance. For grazer abundance, nutrient enrichment effects are BLUPs with model-based Wald 95% CIs, whereas warming and interaction effects are empirical within-site log-scale contrasts plotted with Wald 95% CIs based on propagated within-site uncertainty (see Supplementary Methods (Analyses)). For warming and interaction effects at the non-enriched Madeira site, replication was very low following plate detachments, so propagated uncertainty is effectively zero and the interval collapses to the point estimate.

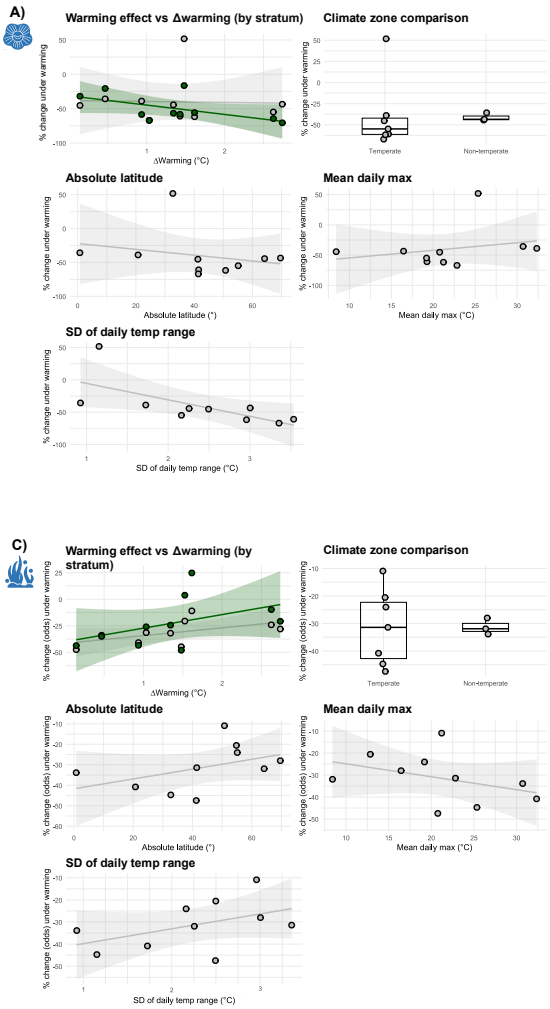
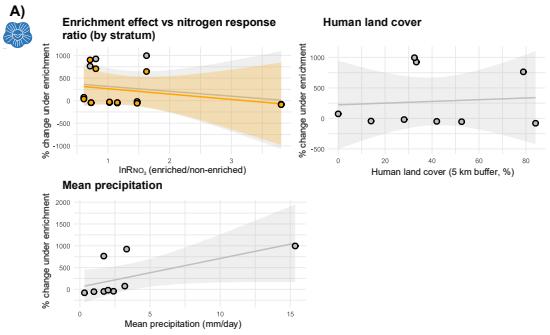


Figure S3 | Warming meta-regression visualisations. Panels summarise how the warming effect varies with moderators (A = barnacle abundance; B = grazer abundance; C = macroalgal cover). ΔWarming (°C) is plotted against the warming effect estimated separately for non-enriched and enriched sites, with separate OLS fits and 95% CI ribbons. Other continuous moderators (absolute latitude, mean daily maximum temperature, SD of daily temperature range) are shown using warming effects estimated from non-enriched sites only, with OLS fits and 95% CIs. Points show site estimates (black-outlined circles). The climate-zone panel is a boxplot (temperate vs. non-temperate) with differences evaluated by two-sided Welch t-tests. Effects are expressed as percent change in mean abundance (barnacles, grazers) or percent change in odds of macroalgal cover.



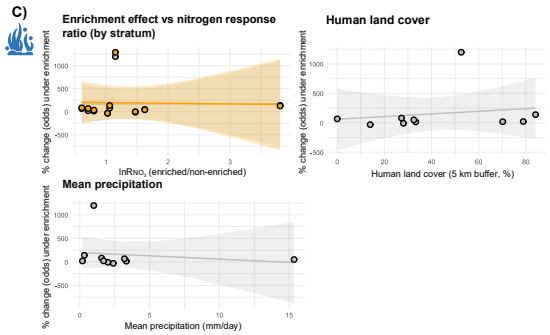


Figure S4 | Nutrient-enrichment meta-regression visualisations. Panels summarise how the nutrient-enrichment effect varies with nitrate exposure and environmental moderators (A = barnacle abundance; B = grazer abundance; C = macroalgal cover). The nitrate response ratio ($lnRNO_3 = \ln(E / NE)$; see Supplementary Methods (Analyses)) is plotted against the nutrient-enrichment effect estimated separately for ambient and warmed plates, with separate OLS fits and 95% CI ribbons. Other continuous moderators (human land cover; mean daily precipitation) are shown using nutrient-enrichment effects estimated from ambient plates only, with OLS fits and 95% CIs. Points show site estimates. Portugal 2 (Porto) is excluded due to near-zero non-enriched nitrate (see Supplementary Methods (Experimental)).

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5

Research Article

Chapter 5 | Balancing the Blue Economy and Multiple Stressor Management in Marine Spatial Planning at the Land–Sea Interface

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5.0 Commentary and statement of authorship

Chapter 5 shifts from empirical diagnosis of multiple stressor effects to considering how coastal governance can be structured to monitor, manage, and mitigate stressors that vary across time, space, and ecological organisation. The chapter is motivated by the recurring empirical messages from the thesis' experimental chapters: stressor effects and interactions vary across biological scales and contexts, expressed through both temporal dynamics and spatial cross-site heterogeneity. The chapter therefore treats multiple stressor management as a governance design problem, asking whether current conventions, frameworks, and tools at the land–sea interface are equipped to anticipate or even consider interactions, indirect pathways, and shifting exposure regimes.

The chapter argues that marine spatial planning (MSP) is a particularly relevant governance framework because it is designed to coordinate competing uses and objectives across space and time, and can be paired with cumulative impact assessment and indicator systems to represent multiple pressures across sectors (Ehler, 2021; Frazão Santos et al., 2024; Hodgson & Halpern, 2019). MSP is treated as a planning process for making trade-offs transparent and adaptive, rather than as a single conservation instrument. The chapter further situates multiple stressor management within blue economy narratives, framing sustainable economic activity as both a driver of independent and interacting stressors, and a potential lever for aligning development with management objectives (Queirós et al., 2021).

The central contribution of this chapter is an eight-component framework intended to integrate multiple stressor management into MSP in a way that is explicit about interactions, pathways, and adaptive triggers. This emphasis on operationalisation exemplifies the chapter's role as an applied synthesis of the prior empirical work alongside the wider literature. To keep recommendations grounded in contemporary governance practice, the chapter operationalises the framework in a Massachusetts (USA) case study developed in partnership with the New England Aquarium. In addition to the main manuscript (§5.0–5.4) and supplementary information (§5.5), a supplementary research brief (§5.6; reformatted for inclusion in this thesis) provides a practitioner-oriented output for Massachusetts to distil key messages and to provide an accessible entry point for diverse users. Notably, the journal in which this manuscript has been accepted (*npj Ocean Sustainability*) intends to feature the paired manuscript and research brief as an exemplar for similar submissions, in order to incentivise practitioner-oriented dissemination beyond the standard format for policy manuscripts.

Chapter 5 concludes the research chapters of this integrated thesis by translating the scientific problem of multiple stressor context dependence into policy and governance terms. It uses MSP to structure how multiple stressors at the land–sea interface and their potential interactions can be represented, prioritised, monitored, and adapted in response to changing conditions, while recognising the economic and sectoral realities that shape local coastal decision-making under global change.

Statement of Authorship

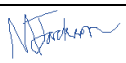
Title of Paper	Balancing the Blue Economy and Multiple Stressor Management in Marine Spatial Planning at the Land–Sea Interface
Publication Status	✓ Published □ Accepted for Publication □ Submitted for Publication □ Unpublished and unsubmitted work written in a manuscript style
Publication Details	Manuscript details Title: Balancing the Blue Economy and Multiple Stressor Management in Marine Spatial Planning at the Land–Sea Interface. Status: Published in *npj Ocean Sustainability* (doi.org/10.1038/s44183-026-00192-3). Author list Ramesh Wilson, Sarah Reiter, Catarina Frazão Santos, Tundi Agardy, & Lisa M. Wedding. Data accessibility statement No new datasets were generated for the current study. For data layers employed in Figure 2, links to live ArcGIS Feature/Map Services are provided in the Supplementary Information. All Massachusetts state data used in this figure are public domain, with sources acknowledged in the Supplementary Information.

Student confirmation

Student Name	Ramesh Wilson (RW)		
Contribution to the Paper	RW co-developed the project concept (with SR & LMW, and later supervisory input from CFS and TA). RW designed the study, made the figures, wrote the full draft of the manuscript, and led revisions, submission, and correspondence. Acknowledged non-author support: A. Gesualdi & J. Chow (New England Aquarium, Massachusetts) for valuable insights on land–sea policy and management within Massachusetts.		
Signature		**Date**	11/01/2026

Supervisor confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor Name and Title	Dr. Michelle Jackson (Associate Professor of Freshwater/Marine Ecology)		
Supervisor Comments	I certify that the candidate made a substantial contribution to the publication, and that the description described above is accurate.		
Signature		**Date**	11/01/2026

5.1 Abstract

Coastal ecosystems face complex, interacting stressors that challenge conventional management strategies. We propose a transformative, eight-component framework considering marine spatial planning, blue economy objectives, and multiple stressor management at the land–sea interface. This framework employs adaptive, data-driven management, holistic ecosystem-based approaches, and stakeholder collaboration to mitigate cumulative impacts across multiple scales. Using Massachusetts (USA) as a case study, we hypothesise ways to apply this framework, enhancing coastal resilience and sustainability.

5.2 Introduction

Coastal ecosystems are among Earth's most productive and dynamic environments, boasting unique ecological processes and high biodiversity at the land–sea interface. They are crucial for nutrient transfer, coastal erosion control, infrastructure protection, and pollution mitigation, and they support both terrestrial and marine food webs (Alongi et al., 1998; Nixon et al., 1996). Vegetated coastal habitats such as mangroves, salt marshes, and seagrass beds stabilise shores by attenuating wave energy, maintaining hydrological balance, trapping sediments, and filtering contaminants from runoff and industrial discharge (Barbier, 2012; Kunze et al., 2021). At the same time, the biodiversity of coastal ecosystems is significant, and is supported by heterogeneous environments that foster diverse ecological communities adapted to fluctuating conditions such as periodic tidal submersion and emersion, which drive thermal stress, desiccation risk, and wave exposure (Kunze et al., 2021). Economically, the ocean underpins fisheries, tourism, transport, and energy sectors, contributing roughly US$2.6 trillion annually to the global blue economy (Organisation for Economic Co-operation and Development (OECD), 2025). As defined by the World Bank, the blue economy refers to the "sustainable use of ocean resources for economic growth, improved livelihoods, and jobs while preserving the health of ocean ecosystems" (World Bank, 2017). With projections indicating that 50% of the world's population will live within 100 km of the coast by 2030, human impacts and resource uses are expected to intensify (Adger et al., 2005).

Coastal ecosystems, and their delivery of valuable goods and services, are inherently variable, experiencing natural fluctuations driven by tidal regimes and seasonal changes. This natural variability can obscure cause–effect signals; distinguishing anthropogenic impacts from background fluctuations therefore requires appropriate baselines and study designs (e.g. 'Before–After Control–Impact' (BACI) designs, environmental gradients) and, where possible, experiments that explicitly incorporate environmental variability (Cooley et al., 2022; Pansch & Hiebenthal, 2019; Seger et al., 2021). Furthermore, coastal ecosystems become especially susceptible to degradation due to the cumulative impacts of multiple stressors occurring simultaneously or sequentially, both from local sources such as urbanisation, industrialisation, and agriculture (leading to habitat loss, pollution, and eutrophication) (Halpern et al., 2008), and global-scale pressures including climate change, sea-level rise, ocean warming, acidification, and changes in ocean circulation, resulting in

shifts in species distributions and losses in ecosystem functions and ecosystem service provision (Doney et al., 2009). Multiple stressors interact in complex and often unpredictable ways, further impacting ecosystems (Jackson et al., 2021; Orr et al., 2020). In broad terms, the effects can be considered additive (sum of individual impacts), synergistic (greater than sum of impacts), or antagonistic (less than sum of impacts), significantly altering ecosystems in unpredictable ways in the case of non-additive antagonisms and synergisms (Carmichael et al., 2025; Carrier-Belleau et al., 2021; Jackson et al., 2021; Orr et al., 2020). This poses challenges for management interventions, requiring a comprehensive understanding of how stressors at both the local and global scales interact against a backdrop of variability at the land–sea interface, to ensure interventions are effective across different spatial and temporal scales (Carrier-Belleau et al., 2021).

Despite their ecological importance and vulnerability, coastal ecosystems remain underrepresented in multiple stressor policy and management frameworks. The 2022 UNESCO Summary for Policymakers on Ocean Multiple Stressors primarily addresses open-ocean and seafloor habitats but overlooks coastal features such as strong salinity gradients, sediment dynamics, and the unique marine–terrestrial connectivity that shapes biodiversity and ecosystem function (IOC-UNESCO, 2022). Major international conventions such as the Convention on Biological Diversity (CBD) (Conference of the Parties to the Convention on Biological Diversity, 2010, 2022), the United Nations Convention on the Law of the Sea (UNCLOS) (United Nations, 1982), the United Nations Framework Convention on Climate Change (UNFCCC) (United Nations, 1992), and the Paris Agreement (United Nations, 2015), offer broad environmental mandates but rarely address coastal zones explicitly or account for non-linear stressor interactions (see Table 1). This gap partly reflects jurisdictional caution, since coastal waters fall under national sovereignty; however, it can neglect ecological connectivity and transboundary impacts, undermining ecosystem-based management across administrative boundaries (de Oliveira, 2023; Popova et al., 2019). Furthermore, marine conservationists have historically emphasised the distinctiveness of marine ecosystems, leading to institutional fragmentation between marine management and terrestrial watershed management (Chilima et al., 2013; Duda & Sherman, 2002). For example, in the European Union, separate frameworks such as the Marine Strategy Framework Directive (European Parliament and Council of the European Union, 2008) (MSFD; achieving 'Good Environmental Status' in marine waters) and the Water Framework Directive (European Parliament and Council of the European

Union, 2000) (WFD; achieving good ecological and chemical status in inland, transitional, and coastal waters through river-basin management plans) coexist, with differing scopes, indicators, and reporting cycles that can complicate coordination at the land–sea interface (European Commission, 2025a). Explicitly bridging terrestrial and marine governance within spatial planning frameworks is essential to effectively manage cumulative stressors across the land–sea interface (Asprogerakas et al., 2020).

International convention	Year of establishment	Summary	Multiple/cumulative stressors	Coastally specific stressors	Coastal habitat differentiation
CBD *Convention on Biological Diversity*	**Adopted:** 1992 **Enforced:** 1993 • Aichi Targets: 2010 • Kunming–Montreal Targets: 2022	*To conserve biological diversity, sustainably use its components, and ensure the fair and equitable sharing of benefits arising from the use of genetic resources.*	Kunming–Montreal Target 7: Abstractly acknowledges the need to "consider cumulative effects" of several pollution types. However, lacks specification for acknowledging non-linear, interactive stressor combinations.	Several targets acknowledge various stressors (Target 5: Wildlife harvesting; Target 7: Pollution; Target 8: Climate change). However, they are addressed more broadly, without direct reference to coastal zone.	Coastal environments somewhat differentiated in Aichi Target 11 and Kunming–Montreal 30 × 30 Target 3, as well as relation to broad land–sea integration. Generally, a greater focus on unspecified marine environments.
UNCLOS *United Nations Convention on the Law of the Sea*	**Adopted:** 1982 **Enforced:** 1994	*To establish a legal framework for all marine and maritime activities, including territorial waters, seabed mining, and the conservation and management of marine resources.*	No explicit reference to the concept of multiple stressors or cumulative impacts. Article 192: Provides a broad mandate for the protection and preservation of the marine environment. Article 194: Addresses reduction of marine pollution.	Article 194: Acknowledges pollution from land-based sources. However, addresses pollution in a broad marine sense without direct reference to coastal zone.	Indirect reference to coastal zones more broadly by reference of pollution mitigation from land-based sources. Generally, a greater focus on unspecified marine environments.
UNFCCC *United Nations Framework Convention on Climate Change*	**Adopted:** 1992 **Enforced:** 1994	*To stabilise greenhouse gas concentrations in the atmosphere at a level to prevent dangerous anthropogenic interference with the climate system, while promoting sustainable development and supporting adaptation and mitigation efforts.*	No explicit reference to the concept of multiple stressors or cumulative impacts. Articles 3 and 4: Emphasise the need to consider interrelationships between various climate-related processes.	Article 4.1(d & e): Acknowledges that coastal areas have specific needs to be considered in climate change adaptation measures. However, they are addressed more broadly, without direct reference to coastal zone.	Coastal environments somewhat differentiated in Article 4.1, with brief reference to integrated coastal zone management in 4.1(e). Generally, a greater focus on unspecified marine environments.
Paris Agreement *Subsidiary UNFCCC treaty*	**Adopted:** 2015 **Enforced:** 2016	*To set goals to limit global warming to below 2°C, aiming for 1.5°C. The Agreement increases global adaptation, aligns financial flows with low greenhouse gas emissions and climate-resilient development, and requires submission of Nationally Determined Contributions every five years.*	No explicit reference to the concept of multiple stressors or cumulative impacts. Article 7: Encourages integrated, holistic approaches to enhance adaptive capacity.	Sets broad ecosystem targets and lacks specific reference to particular biomes and associated context-specific stressors.	No explicit reference to coastal zone. More general focus on unspecified environments and ecosystems.

Table 1 | Summary of international conventions related to sustainable ocean use. Reference to multiple/cumulative stressors, coastally specific stressors, and coastal habitat differentiation evaluated with traffic light coding system: Green = reference to topic present; Orange = partial or indirect reference; Red = inadequate or absent reference.

Marine spatial planning (MSP) is a critical tool for organising and managing marine spaces and has the potential to foster integrated management while balancing competing activities, reducing sectoral conflicts, and protecting ecosystem services (Ehler, 2021; Flannery et al., 2020). MSP's focus on the spatial and temporal distribution of activities differentiates it from other coastal management approaches, making it suitable for addressing multiple stressors whose cumulative impacts and interactions may vary over time and space (Fig. 1). Although MSP requirements vary globally, within the European Union for example, the MSP Directive (2014/89/EU) explicitly requires that maritime spatial plans take account of land–sea interactions (Art. 6(2)(a); see also Arts. 4(2) and 7) (European Parliament and Council of the European Union, 2014). More broadly, applying an ecosystem-based approach within MSP entails systematically considering such land–sea interactions, and where appropriate, aligning with complementary coastal frameworks such as Integrated Coastal Zone Management (ICZM; also known as Integrated Coastal Management (ICM)), ensuring connectivity of open ocean and coastal resources, uses, and stressors across space and time.

Implementing flexible, adaptive strategies that evolve with new scientific insights and dynamic coastal and estuarine conditions is crucial to safeguarding coastal ecosystems and values (Cooley et al., 2022). Additionally, adopting spatial planning approaches that promote sustainable economic benefits and integrate considerations across species, spaces, and sectoral domains into a comprehensive land–sea framework can enhance these strategies' effectiveness (Morzaria-Luna et al., 2020; Wedding et al., 2022). Balancing the development of a blue economy with environmental and social sustainability is vital to ensuring the resilience of coastal ecosystems against a backdrop of interacting stressors at the land–sea interface.

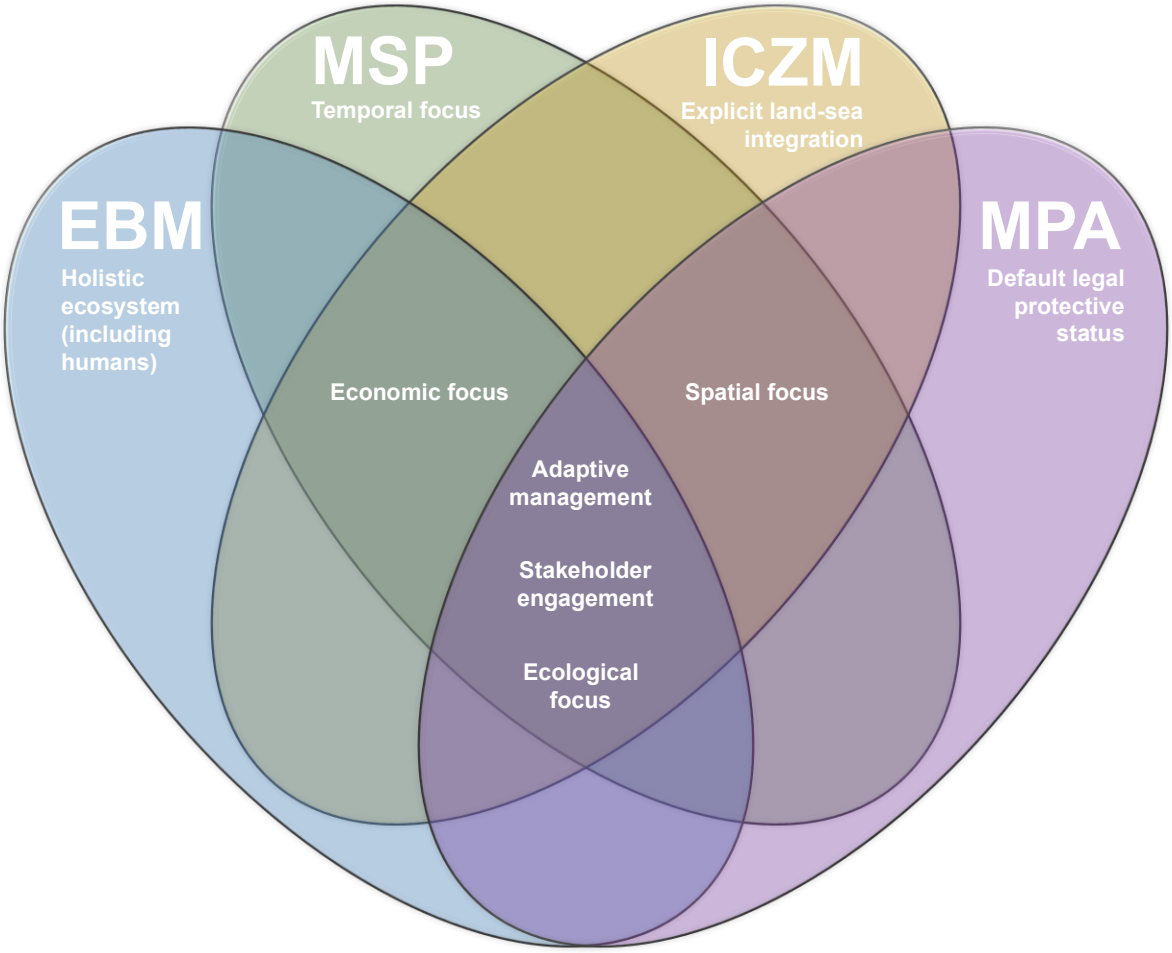


Figure 1 | Four-set Venn diagram illustrating overlaps in core aims of key coastal management approaches. EBM: Ecosystem-Based Management; MSP: Marine Spatial Planning; ICZM: Integrated Coastal Zone Management; MPA: Marine Protected Area.

Here, we propose a framework for balancing blue economy principles with multiple stressor management in MSP at the land–sea interface. Taking inspiration from the key components of climate-smart MSP defined by Frazão Santos et al. (2024), our framework components specifically address stressor interactions at the coastal interface, aligning sustainable economic activities with ecological resilience. Each component follows specific entry points aligned with broader UNESCO MSP guidelines (Ehler & Douvere, 2009) to facilitate operationalisation (SI Table S1). These apply both at the beginning of, and during, the MSP planning and implementation process. We demonstrate this approach through a Massachusetts (USA) case study, identifying practical pathways, challenges, and opportunities for integration within an existing sub-national policy context. Because the United States has no federal statute mandating MSP, and national direction has come via executive policy that has shifted over time (e.g. Executive Order 13547 which promoted coastal and marine spatial planning, and was later superseded by Executive Order 13840

which did not mandate MSP (United States, 2010, 2018)), MSP practice is largely state-led and supported by federal data infrastructure (e.g. the NOAA-BOEM platform) (Bureau of Ocean Energy Management, 2022; NOAA Office for Coastal Management, 2025). We therefore draw recommendations from existing international examples, including the EU MSP framework, as clear reference points, while synthesising within the context of Massachusetts as an illustrative sub-national case study (see Supplementary Information for further case-study rationale and blue economic context, and Fig. 2 for illustrative map of key sectors, coastal activities, and potential overlaps at the land–sea interface). We further provide a Research Brief for Massachusetts that distils the case study into a short, practitioner-oriented summary for policymakers and planners (see Supplementary Document; Research Brief). These components are designed to: 1) promote a holistic approach to managing multiple stressors; 2) ensure integration at the land–sea interface within management frameworks, avoiding gaps that could arise from separating terrestrial and marine considerations; 3) facilitate cross-sectoral collaboration to support long-term sustainability within blue economy objectives.

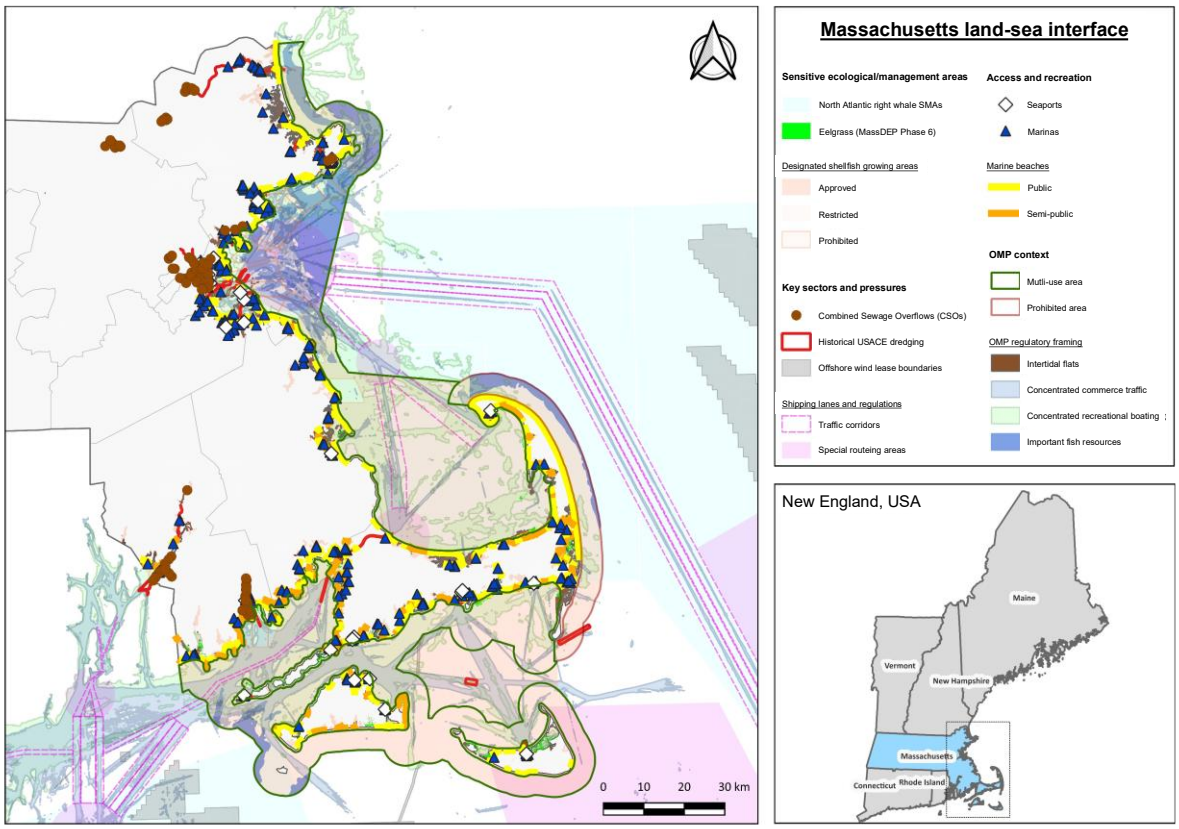


Figure 2 | Activities at the Massachusetts land–sea interface. Illustrative map showing: (i) sensitive ecological/management features (North Atlantic Right Whale Seasonal Management Areas; eelgrass Phase 6; Designated Shellfish Growing Areas by status); (ii) key sectors/pressures (shipping corridors and special routing areas per NOAA ENC; historical USACE dredge footprints; offshore wind lease areas; coastal CSO outfalls within 1 km of the shoreline); (iii) access and recreation areas (seaports; marinas; public and semi-public beaches), and; (iv) 2021 Ocean Management Plan (OMP) context (Prohibited and Multi-Use areas, Mask). Right-hand inset locates Massachusetts within the wider New England region. All geospatial data are retrieved from the most recent publicly accessible GIS feature services. Additional information on map construction, data sources, and data aggregation is provided in the Supplementary Information.

5.3 Balancing the blue economy and coastal multiple stressor management

MSP typically incorporates economic considerations through sectoral coordination, often aligning implicitly or explicitly with goals emphasised by blue economy initiatives (Kidd et al., 2020; Saunders et al., 2020). Initiatives like the High Level Panel for a Sustainable Ocean Economy, comprising 18 nations representing 50% of global coastlines, aim to protect 30% of the ocean by 2030 and sustainably manage 100% of national ocean areas (High Level Panel for a Sustainable Ocean Economy, 2023). At the European level, the 2025 European Ocean Pact has committed €1 billion towards growing a competitive, sustainable blue economy by tightening links between marine planning, investment and open data—explicitly inviting multidisciplinary collaboration across ecology, economics, technology, and governance (European Commission, Directorate-General for Maritime Affairs and Fisheries, 2025). Recent legal and policy signals also push the blue economy toward 'nature-positive' and regenerative practice, including the UN High Seas (BBNJ) Agreement, reaching 60 ratifications in September 2025 (European Commission, Directorate-General for Maritime Affairs and Fisheries, 2025), the ITLOS May 2024 advisory opinion clarifying States' duties under UNCLOS to prevent, reduce, and control marine pollution (International Tribunal for the Law of the Sea, 2024), and the ICJ's advisory opinion in July 2025 clarifying climate-related obligations of states (International Court of Justice, 2025). However, large-scale blue economy strategies frequently prioritise national economic interests (e.g. GDP growth through offshore wind or industrial port development), which may not always align directly with state-level or community-scale interests (Knol-Kauffman et al., 2023). Additionally, many coastal and marine systems function as open-access commons, and without mechanisms such as ocean-assets trusts to ensure shared stewardship, private investment risks exploitative, unsustainable use, and exclusion of traditional users (Hernández-Blanco et al., 2024). Recognising and bridging this gap by harmonising national priorities with local economic sustainability and ecological resilience is essential for effective coastal management, in the face of multiple interacting stressors operating at multiple scales.

MSP and blue economy initiatives already share significant conceptual alignment in their goals of balancing economic activities with sustainable management of marine resources (Osorio-Cano et al., 2019). The blue economy's sector-specific economic focus offers

opportunities to promote enhanced monitoring and data collection (Setiawan & Wahyudi, 2023). Leveraging this could provide practical entry points to integrate sectoral management more explicitly into multi-sectoral MSP frameworks, allowing systematic evaluation of cumulative environmental impacts and enabling more informed management at the land–sea interface.

Despite conceptual alignment, practical approaches often remain fragmented across sectors (Frohlich et al., 2023; March et al., 2024). When blue economy sectors are managed independently rather than integrated into a cohesive MSP framework, economic activities may inadvertently exacerbate ecological impacts (Hammar et al., 2020; Loiseau et al., 2021). Without a data-driven understanding of the non-linear impacts of multiple pressures, management actions at the local level may be ineffective or even harmful. The proposed framework of mutually reinforcing components for balancing blue economy goals alongside multiple stressor management addresses this challenge, optimising the efficacy of MSP initiatives at the land–sea interface. The components are detailed below, together with their potential application to the Massachusetts case study.

5.3.1 Component 1: Promoting research to understand stressor interactions at the land–sea interface

Modern coastal management demands a sophisticated understanding of multiple, interacting stressors. These stressors often produce non-linear, multi-directional ecological effects as resource use intensifies, with frequent non-additive outcomes across studies (Burgess et al., 2021; Jackson et al., 2021). To make responses more predictable and management-ready, we require standardised definitions and terminology, alongside comparable study designs and integrative modelling (Orr et al., 2020). Moreover, because interaction signs and magnitudes are context-dependent across space, time, and levels of organisation, robust inference requires designs and baselines that resolve spatiotemporal structure and mechanism, complemented by experiments that explicitly incorporate environmental variability and extremes (Catford et al., 2022; Pansch & Hiebenthal, 2019; Pirotta et al., 2022; Thomas & Ranjan, 2024; Turschwell et al., 2022).

Cumulative Impact Assessments (CIAs) can provide a foundation for this approach, enabling planners to evaluate how combined pressures linked to blue economy sectors—for example, nutrient/contaminant inputs from coastal development and aquaculture, underwater noise

and vessel-strike risk from shipping and coastal ports, and benthic disturbance from dredging, cable installation and bottom-contact fishing, together with climate drivers, may exceed ecological thresholds across the land–sea interface (Côté et al., 2016; Halpern et al., 2015, 2025; JPI Oceans, 2024). However, in many implementations, such as Sweden's Geographic Information System (GIS) tool 'Symphony', which is used nationally and shared regionally across the Baltic and North Sea, the CIA is functionally additive: mapped pressure layers and ecosystem components are paired via a sensitivity matrix, and cumulative impact in each grid cell is calculated as the sum of the products (Hammar et al., 2020; Järnberg et al., 2023; Swedish Agency for Marine and Water Management, 2020). The assumption of additivity, however, is a core limitation, as responses to multiple stressors are seldom linear. Accordingly, thresholds and sensitivities should be empirically grounded and periodically revisited, and CIAs should integrate spatial and temporal information on physical, ecological, and socioeconomic variables across the land–sea interface; where feasible, mapping should be paired with interaction-aware analyses so that non-additive combined effects are not missed (JPI Oceans, 2024; Piet et al., 2021a; Willsteed et al., 2024).

To be integrative and holistic, it is crucial to embed CIAs and Strategic Environmental Assessments (SEAs) within a broader, systems-science framework. Systems thinking tools such as Sankey diagrams can support visualisation of stressor pathways and energy or material flows (Schmidt, 2008), although often show limitations in depicting dynamic feedback (Geremicca & Bilec, 2024). Furthermore, AI-driven platforms such as ARIES (ARtificial Intelligence for Ecosystem Services), demonstrate how semantic modelling and machine-learning can dynamically integrate diverse datasets and forecast socioecological outcomes in complex coastal systems (Willcock et al., 2018). By coupling traditional assessments with systems-science approaches and AI tools, MSP can more effectively capture the full complexity of multiple stressor interactions, enabling truly adaptive, data-driven decision-making at the land–sea interface.

How Massachusetts could operationalise Component 1

Leveraging this approach in Massachusetts could streamline efforts to map overlapping land–sea pressures in the adjacent Gulf of Maine, guiding protected zone designations and advancing the state's blue economy goals. Although the state employs forward-looking coastal policies, significant gaps remain in addressing the interactive, non-additive effects of stressors within planning evidence and management frameworks. The Gulf of Maine is one

of the fastest-warming bodies of water globally (Pershing et al., 2015). This warming, alongside associated climate-change stressors such as acidification, and direct coastal pressures such as contaminants and nutrient pollution, presents potential interactive stressor effects that are yet unquantified, but could profoundly impact ecosystems and dependent industries at the land–sea interface.

To make this tractable at the land–sea interface, Massachusetts could couple the state Ocean Management Plan (OMP; Volumes One and Two) with spatial layers served via MassMapper/MORIS, embayment nitrogen evidence from the Massachusetts Estuaries Project (MEP), and watershed planning outputs such as the Cape Cod Section 208 Plan, to identify land–sea interaction research hotspots where land-derived nutrient loads intersect ocean warming/heatwave anomalies and intense use corridors (e.g. shipping and port activities) (Cape Cod Commission, 2017; Massachusetts Estuaries Project, n.d.; Massachusetts Executive Office of Energy and Environmental Affairs, 2021a, 2021b; Massachusetts Office of Coastal Zone Management, n.d.). Such hotspots could then become candidates for mechanistic studies (e.g. eelgrass/shellfish performance under combined heat × eutrophication) and pilot cumulative impact analyses that extend beyond simple additive overlays. The OMP Science Framework already highlights commitments to iterative data acquisition and decision support such as comprehensive seafloor mapping and climate adaptation research; however, it does not establish guidelines for cross-stressor analyses or predictive modelling of interactive effects across time and space (Massachusetts Executive Office of Energy and Environmental Affairs, 2021b). Massachusetts could further adopt a CIA-based GIS tool (e.g. Sweden's 'Symphony') to compare planning scenarios, while explicitly pairing it with interaction-aware analyses derived from targeted research efforts, addressing the aforementioned shortcomings in the tool's current additive scope. More adequate predictive modelling based on this evidence across the land–sea interface would support the anticipatory ability of key blue economy sectors including tourism, fisheries, and aquaculture, to mitigate compounded stressor effects, facilitating effective zoning and adaptive operations in sensitive areas (Fang et al., 2024).

5.3.2 Component 2: Integrating across species, spaces, and sectoral domains

Effective coastal management must recognise the interconnectedness of ecosystems, where stressors across the land–sea interface impact species, habitats, and economic sectors in diverse ways. The '3S' framework (Species, Spaces, and Sectors) by Wedding *et al.* (2022) formalises this lens and offers a strategic approach to addressing multiple stressors on ocean systems. This framework emphasises that ecosystem health is influenced not only by individual stressors but by their combined effects across species (biodiversity, community/ecosystem dynamics), spaces (habitats, wider seascapes, migration corridors), and sectors (human activities, blue economy), revealing critical intervention points for policy and management.

Wedding *et al.* propose network modelling as a valuable tool, enabling managers to visualise and quantify relationships among stressors across the 3S domains. Network models provide a tractable way to identify priority areas by pinpointing 'nodes' most sensitive to stressor interactions, guiding effective conservation efforts or regulatory interventions. For example, in their Arctic case study, this approach anticipated compounded effects of global change stressors like climate change and local stressors such as increased shipping, enabling proactive management of vulnerable regions (Wedding et al., 2022).

How Massachusetts could operationalise Component 2

Massachusetts already has a strong foundation through the 2021 Ocean Management Plan (OMP), which delineates Prohibited and Multi-Use areas and operates on a five-year monitor-evaluate-adjust cycle (Massachusetts Executive Office of Energy and Environmental Affairs, 2021b). There are opportunities to enhance multiple stressor management by adopting a holistic lens linking across the 3S framework. Building on this framework, the state could collaboratively apply a 3S lens explicitly at the land–sea interface to prioritise interventions where interacting stressors converge. Practically, this means assembling a '3S network' from existing state and federal datasets (served via CZM's MassMapper/MORIS tool and wider Mapping and Data Management Program) (Massachusetts Office of Coastal Zone Management, n.d.), so nodes (e.g. eelgrass, shellfish areas, SMAs) and edges (traffic density, historical dredging, coastal effluent) could be scored and tracked over space and time (see Fig. 2 for summary of key activities/habitats at the land–sea interface). Publishing these inputs as live services and simple dashboards lets

planners and users visualise trade-offs and ecosystem services, and see where risk accumulates as conditions change.

Within this 3S network, species and habitats may include eelgrass beds (habitat-forming, stress-sensitive), Designated Shellfish Growing Areas (water-quality-dependent), and North Atlantic Right Whale Seasonal Management Areas (protected-species risk). Spaces may include OMP Prohibited/Multi-Use areas and water-dependent use (WDU) concentrations (e.g. commerce traffic, recreation). Sectors could further cover shipping corridors and special routing areas, offshore wind lease footprints, historic dredge footprints (legacy benthic alteration), and coastal CSO outfalls (land-derived inputs) (see Fig. 2). The network could be updated routinely as MassMapper/MORIS and agency partners refresh planning layers, keeping analyses aligned with current conditions. With this evidence base, managers can set clear, pre-agreed triggers that connect network 'hotspots' to familiar measures: seasonal/time-area tools (e.g. regional fishery closures) where risk peaks for particular species or habitats; speed management in SMAs when whale risk is elevated; and routing preferences, setbacks, or buffer adjustments around mapped 'Special, Sensitive, or Unique' (SSU) resources (e.g. eelgrass) where cables, dredging or dense traffic intersect sensitive areas. Embedding these triggers in the OMP's 5-year cycle keeps MSP zoning and operating conditions flexible. When the network shows strengthening linkages or new high-risk nodes, closures, speed measures or buffer changes could be proposed transparently, reviewed and, if warranted, implemented.

Collaboration could be formalised, for example, through a government-convened working group drawing in the Division of Marine Fisheries (fisheries/time-area rules), Department for Environmental Protection (MassDEP; water quality/CSOs), the Clean Energy Center (MassCEC), and port authorities (offshore wind planning/operations), alongside municipal partners to co-design mitigations and share monitoring data. Existing venues such as the Fisheries Working Group on Offshore Wind provide a ready interface between fisheries and energy sectors and could review network outputs and advise on operational responses at the land–sea interface, making collaboration routine and tying decisions to shared, up-to-date evidence (Massachusetts Office of Coastal Zone Management, n.d.).

5.3.3 Component 3: Explicitly incorporate bidirectional interactions at the land–sea interface

Effective coastal management requires taking explicit account of land–sea interactions (LSI) in both directions: how land activities affect marine systems and how sea processes and uses feed back on land (Kidd et al., 2019). This bidirectional framing is widely recognised in broader MSP guidance, such as the EU MSP Directive (European Parliament and Council of the European Union, 2014) which lists LSI among the minimum requirements, and is transversal throughout the remit of our wider recommendations. Internationally, programmes such as the Netherlands' Delta Programme and 'Room for the River' project combine principles of MSP and ICZM, providing models of LSI-aware planning that link watershed management, flood risk reduction, and coastal adaptation, flood risk reduction and coastal adaptation through combined spatial and engineering measures (Van Alphen, 2016); an approach that aligns with a truly bidirectional LSI lens.

Management approaches such as Integrated Coastal Zone Management (ICZM/ICM) traditionally address nearshore pressures (e.g. nutrient and pollutant runoff) (Jiang et al., 2023), yet connections to larger-scale ocean dynamics such as species migrations, currents, and sediment budgets can be missed if LSI is treated narrowly (Kidd et al., 2019; Soria et al., 2014). Evidence from freshwater systems shows that stronger habitat connections boost resilience to multiple stressors by supporting species movement and functional diversity (Bonnaffé et al., 2024). Translating this resilience into practice across the land–sea interface means designing spatial plans that jointly manage upland watershed uses, shoreline development, and marine zones to sustain continuous ecological flows and buffer against multiple stressors (Hammar et al., 2020).

How Massachusetts could operationalise Component 3

Massachusetts shares challenges echoed across many other states and countries, such as rapid sea-level rise, urbanised watersheds, and competing coastal uses. Therefore, adopting a bidirectional LSI layer more explicitly into the OMP review cycle would help bridge current gaps between watershed actions and marine zoning. Practically, this could involve coupling land-to-sea accounting of nutrient and pollutant loads with sea-to-land measures for shoreline change, and integrating those indicators into the OMP's five-year monitor–evaluate–adjust process (Massachusetts Executive Office of Energy and Environmental Affairs, 2021a, 2021b). The state has already made numerous efforts to account for terrestrial

impacts on marine environments, including CZM's Coastal Water Quality and Coastal Habitat programmes, the 'StormSmart' Coasts toolkit, and the MassMapper/MORIS platforms that serve authoritative, map-ready layers to planners and municipalities (Massachusetts Office of Coastal Zone Management, n.d.). Using these platforms to publish a set of LSI indicators such as embayment nitrogen loads vs. ecological thresholds, shoreline-change and flood-risk metrics, and proximity of sensitive waters to outfalls, would make trends visible, incentivise focus on quantifying non-linear stressor interactions across the land–sea interface, and trigger timely management responses under the plan.

Regarding land-to-sea, OMP evidence could directly reference Cape Cod's Section 208 watershed plan and MEP-derived nitrogen targets so that exceedances in embayments reliably flag adjacent marine uses (e.g. shellfish harvest areas, eelgrass SSUs) for review or mitigation (Cape Cod Commission, 2017; Massachusetts Estuaries Project, n.d.). CZM grant programmes could then prioritise stormwater retrofits or nature-based treatments where marine sensitivity is highest. Additionally, for sea-to-land considerations, the 'StormSmart' suite already provides guidance and map tools for sea-level rise, flooding and erosion; codifying living shoreline and beneficial reuse of dredged sediment options (e.g. thin-layer placement to sustain marsh elevation or beach nourishment with suitable material) as preferred measures in high-risk reaches would align shoreline permitting with downstream habitat resilience goals (Massachusetts Office of Coastal Zone Management, n.d.). Embedding these bidirectional indicators in OMP's governance loop keeps actions concrete and adaptive, operationalising existing frameworks across the land–sea interface and tying decisions to transparent, state-maintained data services and programmes.

5.3.4 Component 4: Investing in data collection and data sharing

Effective coastal ecosystem management relies on accurate, timely, and interoperable data, especially at the land–sea interface where terrestrial pressures and marine responses must be analysed together. Robust, cross-domain data collection and sharing underpin MSP decisions about cumulative and interaction-aware stressors across ecological, social, and economic domains. In practice, this means co-registering both land-to-sea, and sea-to-land datasets at appropriate temporal frequencies so planners can detect non-linear, non-additive effects and act before thresholds are crossed. In addition to ecological reference points, such data collection could include socioeconomic and cultural-use datasets (e.g. livelihood dependence, access/use intensity, cultural values, distributional/equity indicators) so managers can align

user requirements to ecological sustainability, and maintain social licence. Without high-quality, standardised, multidisciplinary datasets, MSP risks blind spots that hinder resilience and sustainable growth within the blue economy (Noble et al., 2019). Moreover, the issue of scale must be considered: many LSI indicators (embayment nitrogen, local shoreline change) are local, while MSP decisions are often at the spatial scale of state or regional seas, necessitating reconciliation of data scale and source. A pragmatic approach is a nested design; collect and QA data at local catchment/shoreline units, expose them via interoperable services with clear metadata, and aggregate upward to MSP planning units with reproducible methods. EU guidance on LSI and ecosystem-based MSP supports this workflow, further stressing multi-level governance, common standards, and iterative updates (Bocci et al., 2024; G. Piet et al., 2021b).

Several operational models demonstrate elements of good practice. Portugal's MSP Geoportal publishes maritime, environmental, and socioeconomic layers to support plan implementation and stakeholder access (Portuguese Maritime Ordinance, n.d.). At the regional-sea, multilateral scale, the OSPAR Data and Information Management System (ODIMS) and its Assessment Portal provide standardised protocols, metadata, and web services to share Northeast Atlantic data across contracting parties, reducing duplication and improving transparency (OSPAR, n.d.). Likewise, the International Council for the Exploration of the Sea (ICES) maintains open data policies (CC BY 4.0) and thematic portals spanning biology, environment, oceanography, and underwater noise, providing data infrastructures that directly support cross-sector analyses and long-term trend assessment (International Council for the Exploration of the Sea (ICES), n.d.). Taken together, these examples demonstrate the value of standards, licensing clarity, and live web services for MSP-relevant evidence.

How Massachusetts could operationalise Component 4

Massachusetts has a strong base in CZM's Mapping and Data Management Program, with the MORIS/MassMapper portals providing authoritative, map-ready layers (Massachusetts Office of Coastal Zone Management, n.d.). To make the system fully LSI-aware and interaction-ready, the OMP can foster cross-agency data sharing and publish a small set of LSI indicators and multiple stressor data streams as live services with agreed standards. In practice, that means: setting protocols (licensing, metadata, QA/QC, update cadence) for integrating cross-agency streams such as MassDEP water-quality monitoring, DMF

fisheries/shellfish data, and MWRA outfall data, and receiving-water monitoring alongside coastal habitat/use layers in MORIS; and ensuring indicators can be rolled up from local embayments and municipal shorelines to the OMP planning units used for zoning and review. MassDEP's surface-water portals and MWRA's long-running ambient/outfall monitoring programme already deliver time-series suitable for land–sea indicators (e.g. nutrient/contaminant loads, receiving-water responses). Publishing these via MORIS, cross-linked with DMF resources, would allow planners to test spatiotemporal covariation between pollution events and ecological or catch trends, then supplemented with follow-up analyses (controlled field studies, mechanistic models, or multivariate time-series) to disentangle the relative influence of stressors over time and space (Rawat et al., 2025). Moreover, increasing the frequency and resolution of data collection across physical, biological, and socioeconomic parameters will improve predictive model robustness, while visualising interactive networks could generate testable hypotheses about stressor interactions, laying the groundwork for targeted experimental or modelling follow-up to establish causality.

Across the sea-to-land direction, 'StormSmart'-aligned shoreline datasets (erosion, flood risk) and coastal habitat status (eelgrass, marsh condition) are best published with consistent identifiers so they can be joined to municipal planning layers and OMP management areas, enabling routine scale reconciliation: local metrics inform state-level triggers in the OMP's five-year monitor-evaluate-adjust cycle. To support transparency and reuse, mirroring ICES-style open licensing and OSPAR-style metadata and services could provide an operational stencil, alongside maintaining a single catalogue of LSI indicators in MORIS/MassMapper so municipalities, agencies, and sectors can all pull from the same source of information.

5.3.5 Component 5: Prioritising adaptive, data-driven management

Adaptive monitoring and data-driven management are critical for handling the natural and anthropogenic variability of the land–sea interface and their associated stressors to ensure resilience and continuity of ecosystem services (Queirós et al., 2021). High-frequency, fine-scale data from remote sensing, electrochemical sensors, and IoT (Internet-of-Things) networks capture real-time fluctuations, establish ecological baselines, and trigger management responses (Wei et al., 2021). Additionally, while Long-Term Ecological Research (LTER) programmes provide indispensable context on enduring trends and regime shifts (Miranda et al., 2020), multi-year analysis and publication timelines often limit their direct utility for immediate management decisions (Miranda et al., 2020). Instead, day-to-day

adaptive responses typically draw on more immediate, management-oriented monitoring, such as continuous water-quality sensors, vessel-tracking systems, and automated biological detectors, feeding live data into decision-support dashboards (Ellison et al., 2019; Koronides et al., 2024). In the Baltic Sea MSP, high-frequency monitoring programmes capture physical, chemical, and biological parameters, with data feeding into the Baltic Marine Environment Protection Commission's (HELCOM) decision-making (Brockmann et al., 2008). This allows adaptive adjustments, such as modifying shipping lanes to reduce pollution in sensitive areas. HELCOM's stakeholder integration, including fishers and NGOs, enhances compliance and data accuracy through local insights (Helsinki Commission (HELCOM), 2024). This collaborative approach has improved the region's capacity to manage multiple stressors effectively, demonstrating the importance of adaptive monitoring in sustaining coastal resilience (Reusch et al., 2018).

The temporal scale at which stressor interactions are assessed is crucial, as their significance and directionality can shift over time (Jackson et al., 2021; Pirotta et al., 2022). Additionally, the mode of stressor application, whether 'press' (continuous, chronic stress) or 'pulse' (episodic, acute stress), can also determine ecosystem responses, with press stressors often eroding resilience over time, while pulse stressors can cause abrupt but sometimes reversible shifts (Fong et al., 2020). Moreover, pulse vs. press disturbances have different management implications: pulse shocks may require more rapid, ephemeral responses; whereas press stressors erode resilience and call for more structural measures. Recognising these temporal dynamics ensures adaptive monitoring accounts for both short-term variability and long term trends, improves detectability of shifts in interaction sign/magnitude, and more adequately informs spatial planning and decision-making.

How Massachusetts could operationalise Component 5

In Massachusetts, the CZM already coordinates map-ready evidence via MORIS/MassMapper, but adaptive MSP at the land–sea interface needs those data streams to be integrated with clear objectives, measurable indices, and pre-agreed triggers so managers can adjust allocations in real time while staying aligned with environmental and economic goals (Massachusetts Executive Office of Energy and Environmental Affairs, 2021b; Massachusetts Office of Coastal Zone Management, n.d.). Practically, this means pairing pulse signals (e.g. DMF paralytic shellfish toxin thresholds that close harvest areas; MDPH beach bacteria advisories; dynamic NOAA right whale speed zones) with press

trends (e.g. MWRA outfall/receiving-water time series, buoy and HF-radar records) and publishing them as live layers in MORIS. When monitoring shows ecosystem function declining or risk peaking from overlapping activities, managers could then modify zoning or impose time-area restrictions (e.g. temporary operating conditions, dredging windows, aquaculture adjustments) and then relax them as indicators recover, with all actions reviewed through the OMP cycle. Investing in additional remote sensing and sensor networks strengthens this cadence, crucially supported further by governance integration: set update frequency, QA/metadata, and licensing for cross-agency feeds (CZM with MassDEP/DMF/MWRA, and federal partners for protected-species/traffic), and define a compact dashboard of indices (e.g. biotoxin and faecal-indicator exceedances, marine heatwave intensity, protected species detections, and embayment water-quality status) so natural variability is distinguished from true stressor interactions. Furthermore, integrating diverse datasets into centralised systems enables timely information flow, supporting responsive, evidence-based decision-making (Queirós et al., 2021).

5.3.6 Component 6: Enhancing stakeholder engagement and cross-sectoral collaboration

Engaging diverse stakeholders and fostering cross-sectoral collaboration across the land–sea interface is essential for effective MSP and blue economy integration amid multiple stressors. Because authorities and communities on land and at sea often work in different policy arenas and seldom meet in joint processes, effective land–sea integration requires intentional bridges between them. Incorporating perspectives from local communities, industry representatives, NGOs, and government bodies enhances the legitimacy, acceptance, and inclusivity of management decisions across resource-dependent sectors (Flannery et al., 2018; Papageorgiou et al., 2024). Engagement mechanisms such as workshops, public consultations, and participatory mapping on shared data portals ensure stakeholders are actively involved in co-defining problems and options on both sides of the coastline (Flannery et al., 2018). Additionally, building capacity through education and training empowers stakeholders to engage effectively (Yet et al., 2022). Crucially for multiple stressor management, deliberation should centre on cumulative and potentially non-linear interactions, so that stakeholders prioritise indicators, thresholds, and triggers that make sense at local (embayment/shoreline) scales but roll up to MSP decisions. This involvement would further strengthen adaptive management and responses to multiple stressors by

making stakeholders active partners in monitoring and adjusting strategies based on real-time insights and predetermined LSI indicators.

A balanced blue economy needs social science alongside biophysical analysis. Social research surfaces distributional impacts, equity and justice concerns, cultural values, social licence to operate, and the governance/power dynamics that shape compliance and effectiveness. Using participatory mapping and co-production, plus tools such as social-network and conflict analysis, helps ensure MSP decisions are legitimate, implementable, and durable across the diverse needs of the land–sea interface (Kelly et al., 2019; Veidemane, 2021).

How Massachusetts could operationalise Component 6

In Massachusetts, CZM programs like the Regional Program and Communications Program provide a foundation for interagency coordination and stakeholder engagement (Massachusetts Office of Coastal Zone Management, n.d.). There could be greater emphasis on convening shared-table land–sea processes that bring municipal/watershed authorities and offshore/marine users into the same room. Expanding these frameworks to involve a broader range of stakeholders from the private sector, local communities, and blue economy sectors presents several opportunities. For example, this could be fostered by joint LSI workshops co-chaired by municipalities and watershed groups alongside DMF, port authorities, and offshore-wind representatives (MassCEC/developers), using MORIS/MassMapper as the common, standard map for participatory discussion. The Regional Program, with locally embedded coordinators, supports community engagement on coastal issues (Massachusetts Office of Coastal Zone Management, n.d.), and is well placed to co-host such cross-boundary sessions to surface conflicts and co-benefits of planned management activities across the land–sea interface. Expanding its reach with structured workshops and public consultations could engage fisheries, tourism, renewable energy, and coastal development more fully, and could draw on existing open forums such as the Fisheries Working Group and Habitat Working Group on Offshore Wind Energy as templates for multi-sectoral dialogue (Massachusetts Office of Coastal Zone Management, n.d.).

Involving local communities in monitoring efforts integrates local observations and traditional knowledge, improving data accuracy, credibility, and fostering stewardship (Mamun & Natcher, 2023). Adding public input mechanisms could enhance transparency

and trust, allowing communities and private entities to voice concerns about national actions impacting them; for instance, by posting plain-language summaries and maintaining two-way feedback (surveys, comment trackers) through CZM's Communications Program pages and MORIS item listings as progress develops. While the Communications Program currently focuses on information dissemination (Massachusetts Office of Coastal Zone Management, n.d.), expanding it to facilitate two-way communication, such as online forums and public feedback updates, would connect decision-makers with the public and build stakeholder buy-in by demonstrating how feedback shapes policy within adaptive management. Moreover, to further strengthen collaboration, Massachusetts could integrate structured conflict resolution mechanisms within MSP. A standing LSI advisory council could include representatives from various municipalities/watersheds and sectors/authorities (DMF, MassDEP, port authorities, MassCEC/offshore wind, fishing, recreation, NGOs), with outputs recorded in the OMP's reporting cycle. This approach would formalise how competing ecological and socioeconomic interests are transparently addressed across the land–sea interface, reducing ambiguity and tying collaborative decisions to shared, up-to-date evidence.

5.3.7 Component 7: Integrating principles of climate-smart planning

MSP that prioritises resilience and adaptability to climate-related impacts such as ocean warming, acidification, and sea-level rise—all of which pose significant risks to both ecosystems and economic sectors (Frazão Santos et al., 2024)—has the potential to be most impactful. Climate-smart MSP explicitly recognises climate change as a key stressor, requiring a comprehensive consideration of climate-related impacts, and strategies to minimise them in spatial planning to enhance resilience (Frazão Santos et al., 2024). This is particularly notable in the context of multiple interacting stressors at the land–sea interface, whereby local drivers may be disproportionately impactful against this backdrop of global change. Coastal and marine ecosystems like mangroves, seagrass beds, kelp forests, and rocky shorelines act as natural buffers against storms and support biodiversity, contributing to climate adaptation (Veettil et al., 2021). Furthermore, many of these habitats play a significant role in carbon sequestration and storage, contributing to climate mitigation. Prioritising their conservation within MSP enhances adaptive capacity and promotes long-term resilience (Gattuso et al., 2018).

Climate-smart MSP benefits from integrating future climate scenarios (e.g. warming, sea-level change, weather patterns), fostering cross-boundary collaboration, and using iterative, data-driven approaches to reduce climate risks and protect marine resources. Countries such as Barbados, Sweden, Mozambique, and Ireland incorporate explicit climate considerations into ocean plans, demonstrating how targeted measures like habitat restoration, flexible zoning, and data-driven modelling support mitigation and adaptation, reduce resource-use conflicts, and strengthen socioeconomic resilience under different warming scenarios (Frazão Santos et al., 2024).

How Massachusetts could operationalise Component 7

In Massachusetts, integrating climate-smart approaches into MSP is essential given the rapid regional warming in the Gulf of Maine and the state's vulnerability to sea-level rise (Pershing et al., 2015). Programmes like the 'StormSmart' Coasts Programme already help municipalities adapt to these challenges by focusing on flood resilience and shoreline management guidance (Massachusetts Office of Coastal Zone Management (CZM), n.d.-j), and planners could standardise climate assumptions through a combination of existing tools such as the Massachusetts Coast Flood Risk Model (MC-FRM) scenarios (2030/2050/2070) and the ResilientMass planning and action trackers, to drive consistent screening and updates under the Ocean Management Plan (Massachusetts Executive Office of Energy and Environmental Affairs, n.d.; Massachusetts Office of Coastal Zone Management, n.d.). Leveraging MassMapper/MORIS to overlay sea-level/flood layers with sensitive resources (eelgrass, shellfish, marshes) and sector footprints enables land–sea stress-testing of spatial allocations; adding marine-heatwave intensity layers and dynamic zones for migratory species (e.g. right whales) then allows scenario testing and, where appropriate, time-area adjustments (e.g. routing, timing, or speed measures) when agreed indicators exceed thresholds. Scenario planning and climate risk assessments allow anticipation of ecosystem shifts (Queirós et al., 2021), enabling planners to align blue economy activities with climate goals for greater resilience. For example, fisheries could adjust to species distribution changes due to warming waters, and coastal tourism can be managed to account for seasonal climate variability, preventing ecosystem degradation and ensuring visitor safety (Ojea et al., 2020). Furthermore, the state could incentivise climate-resilient coastal infrastructure investments, such as elevated docks and storm-resistant ports, by directing capital and grant programmes towards projects that reduce exposure and deliver adaptation co-benefits against multiple

stressors, ensuring the long-term sustainability of blue economy activities at the land–sea interface.

5.3.8 Component 8: Aligning existing economic and spatial planning policies

Aligning spatial planning policies across land and sea with blue economy principles is crucial for policy coherence and sustainable coastal development. This involves reviewing and harmonising existing regulations to resolve conflicts and create synergies, thereby establishing a cohesive framework that supports both environmental protection and economic growth (Frazão Santos et al., 2021). Such coherence is essential for achieving goals like ecosystem conservation, economic development, and social equity within shared marine spaces. The European Union's (EU) Directive on MSP (2014/89/EU) (European Parliament and Council of the European Union, 2014) serves as a model for integrating sustainable economic development with MSP, and explicitly notes land–sea interactions. Moreover, the Directive requires member states to incorporate multidisciplinary economic, social, and environmental dimensions into their plans, aligning with the EU's Blue Growth Strategy (European Commission, 2021), and the aim of the 2025 European Ocean Pact to operationalise policy alignment across environment, transport, innovation, and regional development (European Commission, Directorate-General for Maritime Affairs and Fisheries, 2025). This integration promotes balanced marine resource use, resolves sectoral conflicts, and facilitates effective cross-border cooperation.

Recent synthesis of the EU policy landscape for land–sea interactions by Innocenti & Attombri (2024) maps how marine, water, nature, and climate laws interlock and where gaps remain, particularly useful for identifying conflicts and synergies when aligning MSP with terrestrial planning and restoration agendas within a developing blue economy (Innocenti & Attombri, 2024). Streamlining regulatory pathways and simplifying permitting processes enhance compliance and adaptive governance, while mandatory stakeholder involvement ensures transparency and inclusivity. Furthermore, harmonising MSP with restoration and blue-carbon policies, such as habitat rehabilitation mandates and blue carbon initiatives, can help ensure that spatial plans not only manage uses but actively promote ecosystem recovery in degraded coastal and marine areas (Nuyts et al., 2024).

How Massachusetts could operationalise Component 8

The Massachusetts OMP aligns local and national regulations through the CZM Federal Consistency Review, ensuring that state activities affecting the coastal zone are consistent with wider national policies (Massachusetts Executive Office of Energy and Environmental Affairs, 2021a). There is potential to further streamline blue economy frameworks within spatial planning. Enhancing interagency coordination with organisations such as the Massachusetts Environmental Trust and regional programs like the Northeast Regional Ocean Council (NROC) could improve policy coherence across resource use contexts. CZM already participates in Regional Ocean Partnerships (e.g. NROC) to synchronise data and policies across New England; this forum could be used to further align multiple stressor policies at the land–sea interface more explicitly. Increasing their involvement in planning decisions would synchronise blue economy strategies with MSP, fostering a unified approach and ensuring that blue growth aligns with environmental protection. Supporting the development of a blue economy with MSP could be further encouraged through financial incentives such as subsidies and certification schemes, which prioritise environmental stewardship across sectors (Kyriazi et al., 2023). Massachusetts could operationalise this by prioritising LSI-smart projects within existing programmes; e.g. MVP Action Grants for climate adaptation on the landward side, and MassCEC port/workforce investments tied to environmental performance for offshore-wind supply chains. Incentivising sustainable practices in user sectors such as fisheries, tourism, or renewable energy could then be linked more directly to measurable outcomes at the land–sea interface, promoting alignment between economic development and ecosystem health and resilience.

5.4 The future of MSP at the land–sea interface

The challenges facing coastal ecosystems are intensifying due to multiple interacting stressors, rendering traditional management approaches insufficient. The overlapping biodiversity and climate crises, driven by rising sea temperatures, ocean acidification, species loss, and feedbacks that weaken the ocean's carbon sink capacity, underscore the urgent need for a sustainable ocean economy and holistic, adaptive management strategies across the land–sea interface (Ehler, 2021; Morzaria-Luna et al., 2020).

To achieve ecological and socioeconomic sustainability amid anthropogenic change, we propose a transformative MSP framework centred on bidirectional land–sea interactions by embedding eight complementary components into the planning processes. Notably, these components have the potential to be employed even after MSP is underway, as demonstrated by our Massachusetts case study, to yield even greater efficiency and effectiveness. Together, these elements ensure that economic activities proceed in step with ecological and resilience goals, supporting sustainable growth without sacrificing ecosystem health in the face of potentially non-linear, multiple interacting stressors. It is designed to navigate both immediate fluctuations and long term trends, safeguarding coastal and broader marine ecosystems and the livelihoods they support in line with global goals such as Sustainable Development Goal 14 and the Ocean Decade Programme (Reimer et al., 2020; Winther et al., 2020).

Global discussions such as the 16th Conference of the Parties to the Convention on Biological Diversity (COP16) highlight the critical need for this approach across both land and sea. COP16 emphasised translating the Global Biodiversity Framework into actionable steps, including identifying Ecologically or Biologically Significant Marine Areas, to achieve the goal of protecting 30% of land and sea by 2030 (Conference of the Parties to the Convention on Biological Diversity, 2024). However, coastal and marine biodiversity remains underrepresented in conservation efforts, jeopardising ecosystem functions across the land–sea interface vital for carbon storage and climate regulation. Our framework bridges this gap by offering targeted, equitable coastal and marine management strategies that align with COP16 objectives. By emphasising land–sea integration, investing in data, and aligning policies, we facilitate the incorporation of marine considerations into National Biodiversity Strategies and Action Plans, aiding countries in fulfilling their biodiversity commitments.

The future success of MSP and the blue economy depends on adaptability to environmental uncertainties, greater focus on stressor interactions, and cross-sector innovation by bringing land and sea authorities and users to the same table. By adopting this comprehensive, adaptive, and inclusive framework, we can better navigate the complexities of multiple interacting stressors at the land–sea interface. This integration supports international commitments like those reaffirmed at COP16 and promotes a sustainable ocean economy that meets present needs while preserving marine ecosystems for future generations.

5.5 Supplementary information

5.5.1 Massachusetts case study

Case study rationale

Massachusetts serves as an exemplary model for harmonising blue economy principles with MSP. The state features a diverse marine environment with an extensive coastline along the Atlantic Ocean and the Gulf of Maine. According to the 2024 Marine Economy Report, Massachusett's marine economy comprises 5,891 businesses, supports over 86,000 employees, and generated $8.3 billion in GDP in 2021 (NOAA Office for Coastal Management, 2024). Tourism and recreation lead the sector, employing 74% of the marine workforce and contributing 55% of marine GDP. Between 2011 and 2021, the marine economy saw a 16% GDP increase, a 41% rise in average wages, and 9% business growth, reflecting the state's commitment to economic and marine resource sustainability (NOAA Office for Coastal Management, 2024).

Massachusetts demonstrates leadership in marine conservation and sustainable growth through policies such as the Massachusetts Ocean Management Plan (Massachusetts Executive Office of Energy and Environmental Affairs, 2021a, 2021b), which integrates strategic spatial and temporal planning, and Biodiversity Conservation Executive Order No. 618 (Executive Order No. 618, 2023), aligning with international biodiversity goals. Further commitment is evident in an $8 million investment in sustainable marine infrastructure and renewable energy projects, reported by the Healey-Driscoll Administration (Massachusetts Executive Office of Economic Development & Seaport Economic Council, 2023). However, with the issuance of a new federal memorandum in January 2025 that places offshore wind development in limbo (The White House, 2025), the broader U.S. policy landscape remains fluid. Massachusetts has a strong state agency promoting ocean planning, as well as a robust coastal zone management agency and collaborative networks that link these with academic institutions and research centres across the state. Key organisations include: Anderson Cabot Center for Ocean Life; New England Aquarium; Marine Biological Laboratory (University of Chicago); Massachusetts Office of Coastal Zone Management; Northeast Regional Ocean Council; Urban Harbors Institute (UMass Boston); and Woods Hole Oceanographic Institution. Bolstered by research, education, and engagement at NGOs

and non-profit research and conservation organisations such as the New England Aquarium, the state highlights the alignment of marine conservation with sustainable economic growth. Its economic significance, ecological diversity, and proactive management make it an ideal case for evaluating and operationalising the present framework.

Map construction and data rationale

We assembled a statewide map of the Massachusetts land–sea interface (Fig. 2) to illustrate, in a single view, (i) sensitive ecological/management features, (ii) key maritime sectors and pressures, and (iii) the Massachusetts Ocean Management Plan (OMP, 2021) regulatory context. For all data layers, we utilised live ArcGIS Feature/Map Services rather than static downloads, so the figure reflects the most current, authoritative layers and their symbology/attributes at the time of publication, while preserving more streamlined reproducibility. All Massachusetts state data used in this figure (MassGIS/CZM, DMF, MassDEP, MassDOT) are public domain under Massachusetts policy, with source acknowledgement listed below.

The map was constructed in QGIS (3.40 LTR). The project coordinate reference system used was NAD83/Massachusetts Mainland (EPSG:26986) to keep buffering and distance operations in metres. All web services (often published in WGS84 or Web Mercator) were reprojected on-the-fly. We overlaid the 2021 Massachusetts OMP Prohibited and Multi-Use management areas and used the OMP Planning Area Mask as the map frame to align subsequent sectoral and biological layers with current plan zoning and to show where uses are explicitly constrained or allowed. To further populate the scope of the OMP, we illustrate a selection of key regulatory layers within the remit of the OMP, including:

- Intertidal flats.
- Concentrated commerce traffic.
- Concentrated recreational boating.
- Important fish resources.

We chose a selection of three sensitive ecological/management features of statewide policy relevance to visualise, with complementary socioecological relevance across the nearshore including:

- MassDEP Eelgrass, Phase 6 (2019–2023) polygons (most recent eelgrass mapping campaign illustrating wider seagrass habitat condition).
- Designated Shellfish Growing Areas (DMF) polygons (harvest classifications maintained by the Division of Marine Fisheries, demonstrating water quality/food safety management domains). We collapsed the five DMF classes (Approved, Conditionally Approved, Restricted, Conditionally Restricted, Prohibited) into three legend bins; Open (Approved + Conditionally Approved), Restricted (Restricted + Conditionally Restricted), and Prohibited to present status intelligibly at statewide scale while preserving regulatory meaning.
- North Atlantic Right Whale Seasonal Management Areas (SMAs) polygons (federal mandatory seasonal speed-restriction zones to reduce ship strikes, illustrating protected-species risk management).

We similarly mapped representative layers to represent key sectors and pressures at the land–sea interface that occupy meaningful sea space, are commonly referenced in MSP and coastal permitting, and have robust, up-to-date statewide coverage:

- NOAA ENC "Shipping Lanes & Regulations" for traffic corridors (TSS, fairways, recommended routes) and special routing areas (Areas To Be Avoided, Particularly Sensitive Sea Areas, Precautionary Areas). NOAA's service is extracted from official ENCs and is updated weekly, making it the most current public view of federal routing measures. We clipped the national layer to the OMP mask for performance. For readability, we grouped subtypes into (i) traffic corridors (Traffic Separation Schemes/Traffic Lanes, Shipping Fairways Lanes & Zones, Recommended Routes) and (ii) special routing areas (ATBA, PSSA, Precautionary), because individual subtype symbology is visually dense at statewide scale, while providing limited additional insight for our purposes.
- BOEM Offshore Wind Leases (OCS lease outlines) to situate present federal renewable energy footprints.
- USACE historical dredge footprints (polygons to 1998) to depict legacy benthic disturbance in channels/anchorages/harbours; included as a spatial proxy of past alteration of seabeds and inlets.

- MassDEP Combined Sewer Overflow (CSO) outfalls to highlight land-derived pollution nodes near the coastal margin.

Moreover, to further demonstrate the scale of activity at the coastal interface and the incidence of tourism/recreation, we added datasets maintained by state agencies to provide intuitive proxies for where people interact with the coast, including:

- Marine Beaches (public and semi-public).
- Marinas (most recent update, 2019).
- Seaports.

Data sources/web feature services used are as follows:

- Eelgrass (MassDEP Phase 6, 2019-2023): https://www.arcgis.com/home/item.html?id=06aaf0fdd9f54a11b815a169fde88989
- Designated Shellfish Growing Areas (DMF): https://arcgisserver.digital.mass.gov/arcgisserver/rest/services/AGOL/DSGA/FeatureServer
- Right Whale Seasonal Management Areas (NOAA): https://services2.arcgis.com/C8EMgrsFcRFL6LrL/arcgis/rest/services/Seasonal_Management_Areas/FeatureServer/3
- ENC "Shipping Lanes & Regulations" (NOAA): https://encdirect.noaa.gov/arcgis/rest/services/NavigationChartData/MarineTransportation/FeatureServer/0
- BOEM Offshore Wind Leases: https://services7.arcgis.com/G5Ma95RzqJRPKsWL/ArcGIS/rest/services/Wind_Lease_Boundaries__BOEM_/FeatureServer
- USACE Dredge Projects (historical): https://services1.arcgis.com/7iJyYTjCtKsZS1LR/arcgis/rest/services/Dredge_Projects_USACE_HIstorical_to_1998/FeatureServer

- MassDEP CSOs: https://services1.arcgis.com/7iJyYTjCtKsZS1LR/arcgis/rest/services/MassDEP_CSOs_2/FeatureServer/0
- Marine Beaches: https://arcgisserver.digital.mass.gov/arcgisserver/rest/services/AGOL/Marine_Beaches/FeatureServer
- Marinas (2019): https://services1.arcgis.com/7iJyYTjCtKsZS1LR/arcgis/rest/services/Marinas_2019/FeatureServer
- Seaports: https://gisstg.massdot.state.ma.us/arcgis/rest/services/Multimodal/Seaport/MapServer/0
- Massachusetts OMP (2021): https://services1.arcgis.com/7iJyYTjCtKsZS1LR/arcgis/rest/services/OMP_2021_18Nov2021/FeatureServer
- New England state outlines: https://arcgisserver.digital.mass.gov/arcgisserver/rest/services/AGOL/NewEnglandStates/FeatureServer

5.5.2 Supplementary tables

Key component	Foundational/operational	UNESCO MSP guide planning stage (Ehler & Douvere, 2009)
Promote research to understand stressor interactions at the land–sea interface	Foundational	NA
Integration across species, spaces, and sectoral domains	Foundational	NA
Explicitly incorporate bidirectional interactions at the land–sea interface	Foundational	NA
Invest in data collection and sharing	Operational	• Defining and Analysing Existing Conditions (Step 5) • Monitoring and Evaluating Performance (Step 9)
Prioritise adaptive, data-driven management	Operational	• Defining and Analysing Existing Conditions (Step 5) • Defining and Analysing Future Conditions (Step 6) • Monitoring and Evaluating Performance (Step 9) • Adapting the Marine Spatial Management Process (Step 10)
Stakeholder engagement and cross-sectoral collaboration	Operational	• Organizing Stakeholder Participation (Step 4) • Preparing and Approving the Spatial Management Plan (Step 7) • Implementing and Enforcing the Spatial Management Plan (Step 8) • Adapting the Marine Spatial Management Process (Step 10)
Integrate principles of climate-smart planning	Operational	• Defining and Analysing Existing Conditions (Step 5) • Defining and Analysing Future Conditions (Step 6) • Monitoring and Evaluating Performance (Step 9) • Adapting the Marine Spatial Management Process (Step 10)
Align existing economic and spatial planning policies	Operational	• Preparing and Approving the Spatial Management Plan (Step 7) • Implementing and Enforcing the Spatial Management Plan (Step 8)

Table S1: UNESCO MSP entry points aligned with key components.

5.6 Supplementary document: Research brief

Department of BIOLOGY
UNIVERSITY OF OXFORD

Balancing the Blue Economy and Multiple Stressor Management in Marine Spatial Planning at the Land-Sea Interface

Massachusetts could serve as a case-study for balancing Marine Spatial Planning and Blue Economy initiatives to support coastal resilience and sustainable growth.

Coastal ecosystems provide many services, including biodiversity, coastal protection, and supporting local economies. However, these ecosystems face increasing local-level stressors, compounding the effects of global stressors in unpredictable ways across the land-sea interface. What happens at the coastal zone affects all interconnected life across the land-sea interface. With the combined impacts of co-occurring human stressors mounting, we must develop actionable strategies at different spatial and temporal scales to mitigate these impacts and protect these critical ecosystems.

In the United States, the National Strategy for a Sustainable Ocean Economy (NSSOE) and the Ocean Climate Action Plan (OCAP) provide comprehensive frameworks for marine coastal management. As one of 18 nations in the High-Level Panel for a Sustainable Ocean Economy, the US has demonstrated its commitment to sustainable ocean management practices within blue economy frameworks. Aligning Marine Spatial Planning (MSP) with Blue Economy initiatives can synergize economic and environmental outcomes across at the land-sea interface. This is particularly beneficial for coastal shorelines, representing an intricate network of sectoral activities across land and sea, such as fishing, tourism, and offshore renewable energy development. By managing the spatial distribution of uses, MSP helps ensure that resource use contributing to the Blue Economy is sustainable and equitable, supporting the resilience and prosperity of coastal ecosystems and the communities that rely upon them.

Massachusetts offers a valuable case-study for harmonizing MSP goals with blue economy initiatives. Its 1500+ mile coastline is a dynamic intersection of biodiversity and associated uses, including commercial fishing, port activities, and tourism.

KEY POINTS FOR POLICYMAKERS

Invest in data collection and sharing

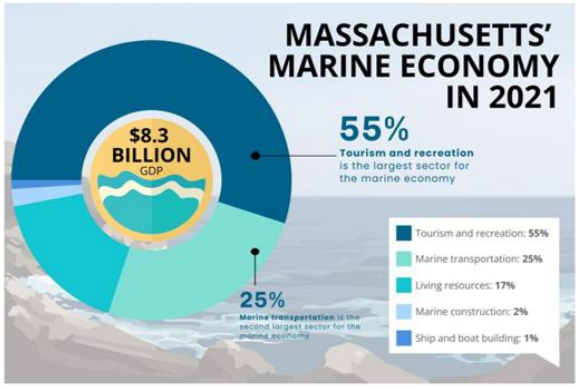
Increase investment in standardized data collection and sharing methods that track multiple stressors at coastal zones and explicitly link land-to-sea with sea-to-land indicators. Coordinated data efforts across state and federal agencies could facilitate evidence-based decision-making and ensure that policies are informed by the most accurate site-specific ecological and socio-economic data. Efforts should also support research into knowledge gaps on emerging stressors and encourage the development of predictive tools and interaction-aware research and analysis.

Prioritize iterative monitoring and management

Implement flexible and dynamic governance strategies that allow adaptive responses to coastal ecosystems' unique and changing nature, and their uses. Marine Spatial Planning frameworks should incorporate iterative monitoring and management, enabling policies to adjust in response to new data and research insights on the cumulative and potentially disproportionate effects of stressors, such as coastal erosion, nutrient runoff, and the broader impacts of climate change.

Integrate across species, spatial, and sectoral management domains

Develop and align policies to explicitly address the integration of land-based and marine impacts, particularly at the coastal zones where human activities overlap intensely. This could be facilitated through a 'species-spaces-sectors' (3S) approach, whereby interactions between these domains are holistically addressed across the broader ecosystem. This could help ensure that spatial planning measures are environmentally and economically effective across the land-sea interface, supported further by shared mapping services and decision-making that convene multisector stakeholders.



State-level policies and programs, including the Ocean Management Plan (OMP) and Coastal Habitat Programme (CHP) address ecological conservation and sustainable economic growth. While the state's existing frameworks offer significant protection for broader coastal areas, the explicit focus on shoreline differentiation and their unique challenges could be enhanced. Strengthening these policies to address the idiosyncrasies of the coastal zone more directly would further ensure that these critical habitats receive targeted attention and effective management strategies. Furthermore, expanding current single-stressor-oriented initiatives, such as the Coastal Pollutant Remediation Grant Program, to emphasize interactions of local human impacts against a backdrop of global change, could enhance the resilience and productivity across the land-sea interface.

Massachusetts spatial planning frameworks are well positioned to effectively integrate spatial tools with Blue Economy initiatives. The OMP can act as a principal planning framework, which already delineates specific zones for various use activities, helping to ensure economic use projects are strategically located to minimize environmental impacts. There is an opportunity to align these spatial zones further with Blue Economy initiatives to create a more cohesive management strategy rooted in holistic sustainability. Programs and initiatives can effectively utilize spatial planning tools like GIS (Geographic Information Systems) for habitat zoning to designate economically sustainable multi-use areas. Combined with the Massachusetts Coastal Zone Authority's emphasis on adaptive, data-driven management, incorporating these tools creates a solid foundation for strategically managing resources across species, spaces, and sectors. A spatially-optimised approach can enhance the placement of economic activities while simultaneously flagging interactive stressors and encouraging coastal resilience.

The expected outcomes of Marine Spatial Planning, Blue Economy objectives, and multiple stressor management are significant. This integrated approach could greatly facilitate the management of multiple stressors, allowing sensitive coastal ecosystems to withstand environmental changes and human impacts better. Sustainable economic growth may be fostered by ensuring that ocean activities are aligned with ecosystem health, thereby securing the long-term viability of sectors. Massachusetts is positioned to use its existing management plans in tandem with Blue Economy initiatives underway in the Commonwealth to effectively manage and protect coastal ecosystems. By addressing the unique needs of its coastal zone and the communities that rely upon them, the state clearly demonstrates potential for fostering a truly sustainable Blue Economy against a backdrop of both local and global change.

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6

Discussion

6.1 Overview and key findings

This thesis develops an integrated synthesis of how coastal ecosystems respond to multiple interacting stressors and how that evidence can be translated into stronger, interaction-aware governance and planning at the land–sea interface. Chapters 3 and 4 provide novel, complementary *in situ* experiments that combine a local nutrient enrichment gradient with an anticipatory warming manipulation, thereby linking near-term management concerns with longer-term, chronic warming effects, consistent with calls for research to jointly address global and local stressors in marine systems (Brown et al., 2013; Gissi et al., 2021; Kunze et al., 2021). Chapter 5 then expands the scope of this foundational experimental work from ecological insights to policy action, proposing a new framework for marine spatial planning that explicitly incorporates multiple stressor interactions, land–sea connectivity, and the emerging blue economy, aligning with wider calls to strengthen the science–policy interface

to better manage multiple stressors (Ehler, 2021; IOC-UNESCO, 2022; Wedding et al., 2022).

Taken together, these research chapters advance the field by showing more clearly that multiple stressor outcomes on rocky shores are not fixed properties of a given stressor pair, but depend on when, where, and at what level of biological organisation they are measured. Specifically, this thesis demonstrates that warming × nutrient enrichment effects can shift within a season, vary across sites at global scales, and be mediated by indirect biotic pathways rather than direct stressor effects alone. It further shows that this variability is not just ecological complexity to be acknowledged, but a tractable feature that can be incorporated into marine planning through interaction-aware, land–sea integrated governance.

Across the experimental chapters, the local UK study in Chapter 3 demonstrates that stressor effects, both independent and interactive, can be strong, temporally structured, and variable across levels of biological organisation. These insights are consistent with syntheses showing that multiple stressor outcomes largely depend on timing, magnitude, and biological context (Jackson et al., 2021; Turschwell et al., 2022). By combining responses across a wide range of biological levels, Chapter 3 links community trajectories to mechanistic response pathways within the same factorial design, advancing a critical research gap in marine ecosystems (Gissi et al., 2021). Furthermore, time-series analyses conducted in Chapter 3 resolve seasonal dynamics across several mid-tide functional groups, separating baseline seasonal trajectories from treatment effects through interaction-aware inference about within-season change. These novel temporal findings align with methodological syntheses that emphasise the need to consider temporal resolution alongside stressor dynamics (Jackson et al., 2021; King et al., 2022; Orr et al., 2024).

Chapter 4 extends this methodological and inferential approach from a single-shore time series, to a globally distributed experiment across 22 international sites. This study provides empirical insights on site-level deviations from global mean responses, abiotic moderator analyses, and path analysis of both direct and indirect biotically mediated pathways, addressing a critical research gap on multinational, coordinated experimental approaches that capture context dependence and improve transferability of intertidal stressor impact inference (Hawkins et al., 2020; Mieszkowska et al., 2019). Recent governance analyses argue that marine spatial planning requires explicit integration across scales, sectors, and knowledge

systems (Bocci et al., 2024; Flannery et al., 2020; Kidd et al., 2020; Ramieri et al., 2019), establishing the importance of the thesis-wide evidence base that coastal stressor outcomes are contingent on spatial, temporal, and biological context.

Building on this critical need, Chapter 5 then situates these empirical and interpretive insights within planning and governance contexts, using the land–sea interface as the focal domain because pressures, responses, and trade-offs that propagate across land and sea require vast cross-sector coordination. Massachusetts was selected as the case study because it combines a mature ocean-planning architecture, a large and growing marine economy, substantial ecological and sectoral diversity across the land–sea interface, and a strong institutional network linking state agencies, regional bodies, and research organisations. This made it a useful real-world test case for asking whether an interaction-aware framework could be operationalised within an active planning system, rather than proposed only in abstract terms. The novel science–policy framework developed in this chapter is consistent with MSP's requirement to account for land–sea interactions (European Parliament and Council of the European Union, 2014), and with long-established evidence that land-derived inputs (including nutrient enrichment and contaminants) structure nearshore ecosystem function and services (Maúre et al., 2021; Nixon et al., 1996; Savage, 2005).

6.2 Implications and future directions

6.2.1 Conceptual and analytical principles for interpreting multiple stressors

A key implication of the experimental work presented in this thesis is the need for greater standardisation and transparency in how multiple stressor interactions are defined, visualised, and communicated across studies and decision contexts. This need is particularly acute at the land–sea interface, where stressors arise from multiple sectors, operate across jurisdictional boundaries, and are interpreted through different disciplinary and management paradigms (Preston et al., 2025). Reviews show that interaction terminology varies widely, that null models are often implicit (that is, unstated and therefore assumed rather than explicitly specified), and that interpretation can change depending on whether effects are evaluated on

additive, multiplicative, or other scales (Crain et al., 2008; Piggott et al., 2015; Schäfer & Piggott, 2018; Spake et al., 2023). Chapters 3 and 4 operationalise an interpretation approach that places directionality and ecological meaning at the centre, supported by conditional stressor-effect visualisations (i.e. predicted outcomes under each stressor combination, displayed as simple effects and their departures from an explicit null) and marginal contrasts that make interaction outcomes interpretable as context-specific deviations from a stated expectation. Such tools are consistent with best practice guidance that interaction terms should be interpreted through predicted outcomes rather than statistical coefficients alone (Duncan & Kefford, 2021; Spake et al., 2023). Furthermore, the use of an equivalence band in Chapters 3 and 4 to distinguish substantively meaningful departures from near-additive (null) outcomes provides a practical solution to address concerns that apparent interaction prevalence can be inflated by sampling limitations, short gradients, or small effect sizes, and supports clearer synthesis by separating statistical detectability from ecological relevance (Lakens, 2017; Mack et al., 2022). Together, these choices emphasise that an apparent 'interaction' is not a single property of a coefficient, but a statement about the scale, the null model, and the ecological interpretation. Making those choices explicit enables collective understanding and interpretation across heterogeneous designs and endpoints.

A further contribution of this work addresses the need to tighten the conceptual and quantitative relationship between cumulative impact assessment and interactive effects. Global cumulative impact mapping has been central to prioritising management action across scales, yet it commonly relies only on additive aggregation of abstract pressure layers, as interaction information is scarce, difficult to parameterise, or not transferable across spatiotemporal contexts (Halpern et al., 2015, 2025; Hodgson & Halpern, 2019). Recent global projections emphasise that cumulative ocean impacts are expected to rise substantially by mid-century, and they explicitly note the challenge of representing non-additive interactions at the global scale (Halpern et al., 2025). At regional scales, however, emerging work demonstrates that interaction-informed cumulative impact assessments can materially change impact estimates relative to additive assumptions, implying that the gap between cumulative mapping and interactive ecology can be narrowed through targeted empirical and modelling advances (Stockbridge et al., 2025), as further demonstrated and incentivised across the scope of empirical analyses within this thesis.

Chapters 3 and 4 contribute to this agenda by producing interaction classifications and moderator structures that can be used as evidence-informed expectations to parameterise sensitivity analyses or uncertainty bounds in cumulative frameworks, rather than requiring fully mechanistic global models for every receptor–stressor pairing. In practical terms, the thesis outputs can be used to identify where and why additive aggregation is likely to be most misleading, and to test the robustness of decisions from empirical sign, timing, and context dependence. This is consistent with arguments that stressor management should explicitly consider interactions between global and local pressures in order to avoid mis-prioritisation and improve the effectiveness of local interventions under climate change (Brown et al., 2013; Côté et al., 2016; Simmons et al., 2021). Accordingly, this thesis supports a pragmatic pathway in which cumulative assessment continues to provide broad-scale prioritisation, while interaction evidence is incorporated where it is most decision-sensitive, particularly in coastal systems where stressors across land and sea converge, or where interventions are likely to change one driver without materially changing the other, so that outcomes are evaluated against interaction-aware expectations rather than implicitly assuming the unmanaged driver is constant or negligible (Carrier-Belleau et al., 2021; Glibert, 2020; Sinha et al., 2017).

Synthesising across Chapters 3 and 4, this thesis advances a set of analytical priorities for future multiple stressor research. First, interaction inference should increasingly be linked to causal attribution and pathway structure, rather than remaining at the level of net effects, consistent with calls to advance causal inference in ecology and improve detection and attribution of ecosystem change (Kong et al., 2025; Pirotta et al., 2022; Schrodt et al., 2025). This thesis advances this agenda, by emphasising abiotic moderators, timing, and indirect biotic pathways as mechanisms by which stressor pairings can produce different outcomes across space and time. Second, modelling frameworks that represent stress responses through performance curves and stressor-dependent non-linearity offer a coherent way to reconcile heterogeneous interaction outcomes when stressor intensity varies or thresholds are approached (Carmichael et al., 2025; Ostrowski et al., 2022; Vos et al., 2023). While Chapters 3 and 4 do not fit performance-curve models directly, they provide the type of empirical leverage that such approaches require, namely within-season resolution of when interaction risk peaks, and cross-context comparisons that isolate candidate moderators of interaction sign and magnitude. Third, experimental design guidance increasingly emphasises that informative multiple stressor experiments require careful choice of gradients, replication,

and endpoints (Orr et al., 2020; Sasaki et al., 2025; Thomas & Ranjan, 2024). Chapters 3 and 4 can serve as templates for balancing tractability with ecological relevance across scale, specifically by pairing a standardised, passive warming manipulation with meaningful real-world contrasts in enrichment context, and by choosing endpoints that reflect both community structure and function across the summer window in which warming and enrichment risks are expected to peak.

6.2.2 Advancing experimental and observational methodologies

Methodological progress is needed to balance experimental realism with feasibility and scalability, so that inference can move from component-level effects toward ecosystem-relevant outcomes without losing interpretability. Recent syntheses in aquatic experimental ecology emphasise that field experiments remain essential for capturing natural variability and community processes, but that feasibility constraints shape design choices, replication, and the types of stressor gradients that can be implemented (Gerhard et al., 2023; Sasaki et al., 2025). The two experimental chapters in this thesis demonstrate for the first time, the feasibility of an *in situ* multiple stressor experiment at the land–sea interface, deployed as both a detailed local time series, and as a globally replicated protocol. This approach actively supports the broader argument that tractable test systems such as rocky shores can generate generalisable field insights when designs are standardised, scalable, and paired with environmental context data (Hawkins et al., 2020, 2023). Comprehensive scientific insights, however, should be encouraged and acquired across a portfolio of experimental approaches: tightly controlled systems (e.g. laboratory experiments) for mechanism and dose-response clarity, paired with scalable field and/or mesocosm platforms for realism, spatial transferability, and policy relevance (Gerhard et al., 2023; Sasaki et al., 2025; Stewart et al., 2013; Ullah et al., 2024).

Building on the thesis' scalable experimental methodology and multi-scale inference (Chapters 3 and 4), future work can build on the experimental foundation presented in this thesis by extending the factorial field design across additional ecological gradients that are known to shape stressor outcomes at the coastal zone, including tidal elevation, wave exposure, shading, and substrate heterogeneity, each of which influences thermal stress and community assembly in intertidal habitats (Gedan et al., 2011; Román et al., 2020; Wang et al., 2020). Incorporating explicit zonation in future deployments (e.g. replicated arrays across low, mid, and high intertidal levels) would allow interaction structure to be tested against a

biologically meaningful gradient in exposure regime, consistent with long-standing intertidal theory that community outcomes reflect the balance between physical stress and biotic interactions across elevation (Helmuth, 2002; Helmuth et al., 2006; Jonsson et al., 2006; Wethey, 2002).

In parallel, future experimental field designs can increase mechanistic resolution by expanding stressor characterisation beyond nutrient enrichment proxies, recognising that sewage-associated stressors include chemical mixtures, pharmaceuticals, endocrine disruptors, and pathogen dynamics that may interact with warming through physiology, immunity, and food-web pathways (Balbi et al., 2021; Cabral et al., 2019; Cabral-Oliveira et al., 2014; Schäfer et al., 2023). Crucially, this is also a feasibility issue: richer characterisation often requires additional probes, water chemistry, and logistics that may trade off against replication or geographic spread. A productive direction is to develop tiered characterisation, i.e. a minimal suite of common foci that preserves comparability across sites, paired with a wider suite of abiotic variables sampled at sentinel sites that anchor deeper interpretation and validate proxy choices. Additionally, where feasible, coupling field experiments to additional biomarker and transcriptomic approaches (building from the thesis' own components) can help identify further pathway-level interactions and cross-tolerance mechanisms, including repeated sampling across time windows and receptor groups, and sampling aligned to standardised aerial exposure histories to separate thermal extremes from desiccation or tidal-emersion context (Brasseur et al., 2022; Clark et al., 2018; Collins et al., 2021, 2023). Moreover, a complementary extension is to broaden the responses investigated beyond the scope of this thesis, including additional barnacle morphology (e.g. height as well as rostro-carinal diameter), condition metrics (e.g. biomass), microbial biofilm composition, and diversity-oriented summaries where appropriate, so that interaction inference can be linked to both community structure and functional consequences while remaining comparable across distributed deployments.

Building on the season-wide findings across Chapters 3 and 4, a clear next step is to resolve how settlement processes and early life stage sensitivity contribute to observed community responses. Reviews of early life stages show high sensitivity to multiple abiotic stressors and highlight the need for recruitment-focused designs that link settlement outcomes to later community patterns (Giménez & Jenkins, 2013; Lathlean & Minchinton, 2012; Przeslawski et al., 2015). Barnacle cyprids respond to surface properties and conspecific cues, implying

that substrate material, texture, and biofilm development may shape recruitment responses to experimental infrastructure, particularly where installations use artificial structures (Burden et al., 2014; Ellrich et al., 2020; Mondal et al., 2021). This points to a practical methodological extension in which future passive warming methodologies are paired with controlled variation in surface rugosity and material chemistry, enabling recruitment preference and stressor-interaction hypotheses to be tested within the same field platform, and providing design-relevant evidence for eco-engineering interventions such as habitat-enhancing coastal infrastructure (i.e. 'living seawalls').

Building on the thesis' combination of replicated in situ experiments, and the adaptive management focus developed in Chapter 5, a key priority is to couple field research with emerging monitoring and data-assimilation approaches. Nearshore and intertidal environments remain challenging for remote sensing due to spatial resolution limits, turbidity, and complex coastlines, yet progress in coastal earth observation and machine-learning-based ecosystem inference suggests growing opportunities to integrate field experiments with scalable observation systems to extend covariate coverage and hazard detection, particularly where data scarcity can otherwise limit inclusive global inference (Brockmann et al., 2008; Palola et al., 2025; Willcock et al., 2018). This supports a future research agenda in which distributed field experiments provide high-quality ground truth for coastal indicators, while remote sensing and automated sensors expand spatial coverage of key abiotic covariates and hazard signals (e.g. surface temperature anomalies, turbidity/chlorophyll proxies, wave exposure, and event timing) and enable early warning and adaptive management triggers, aligning with the adaptive management emphasis of climate-smart ocean planning and reinforcing the Chapter 5 emphasis on adaptive management rather than static planning (Frazão Santos et al., 2024; IOC-UNESCO, 2022; Pershing et al., 2015).

6.2.3 Equitable management, planning, and practices across scales

Distributed field experimentation is also a capacity and equity challenge, as the evidentiary base for multiple stressor management remains geographically uneven (Gissi et al., 2021; Thyrring et al., 2025). Analyses of marine research representation highlight persistent under-representation of many regions and the need to avoid exploitative collaboration models, while horizon scanning work in rapidly changing regions underscores that international coordination must be paired with equitable capacity-building and shared decision-making

(Dahdouh-Guebas et al., 2003; Thyrring et al., 2025; Tolochko & Vadrot, 2021). Chapter 3 supports open and scalable uptake by providing a supplementary build manual for the passive-warming plates, enabling consistent replication and lower-barrier deployment across sites and research groups. Building on this, Chapter 4 acts as a practical model for how global *in situ* experiments can improve representation by not assuming uniform capacity, and by making transparent the associated logistical, financial, and capacity costs. Methodological protocols established in Chapter 4 were designed to be robust to heterogeneous capacity and infrastructure while still producing comparable outputs, aligning with broader shifts toward more inclusive and participatory approaches in environmental monitoring (Haugen et al., 2024; Mamun & Natcher, 2023; Saunders et al., 2020; Yet et al., 2022). Chapter 5 extends this by treating equity and participation as explicit conditions for usable evidence, because interaction-aware planning depends on the incorporation of diverse knowledge across sectors and scales.

The translation of experimental evidence into multiple stressor policy application is most explicitly developed in Chapter 5; however, Chapters 3 and 4 also contribute independent insights by which interaction-aware ecological evidence can strengthen planning and assessment. Cumulative effects assessment is increasingly expected within marine planning and project licensing, yet operational guidance often treats combinations as aggregations rather than explicitly addressing the conditions under which non-additive outcomes are likely, or how they would be tested and communicated in practice (Halpern et al., 2025; Willsteed et al., 2017, 2024). For example, UK guidance for nationally significant infrastructure projects (NSIPs) frames cumulative effects around identifying other actions and describing combined impacts, but provides limited operational specificity on diagnosing or representing interaction types (Planning Inspectorate, 2024). In parallel, the Marine Management Organisation's strategic approach for scoping cumulative effects assessment provides a structured process for identifying pressures and receptors, but leaves a methodological gap between acknowledging combined effects and diagnosing interaction effects in quantitative assessment (Willsteed et al., 2024). A practical implication of the experimental thesis components is therefore to supply and encourage the use of salient intermediate products (e.g. interaction typologies, timing information, and moderators) that can be incorporated into scoping and scenario evaluation, so that stressor interaction-awareness becomes operational rather than purely rhetorical.

A further UK-facing opportunity concerns the current disconnect between public health monitoring and ecological condition nearshore. Bathing water regimes are designed primarily around microbial risk and human exposure, while ecological outcomes at bathing sites (and their sensitivity to interacting stressors) are not typically assessed in a way that supports biodiversity-oriented planning (Palmer & Stapleton, 2023; Whelan et al., 2022). The current policy debate around bathing-water standards and classifications illustrates both the prominence of these programmes and the potential to widen their scientific evidence base beyond compliance alone. A pragmatic pathway, aligned with the thesis' emphasis on cost-effective, interaction-sensitive community metrics, would be to pilot co-monitoring at selected sites alongside existing programmes: pairing existing regulatory microbiological monitoring (faecal indicator bacteria, specifically *E. coli* and intestinal enterococci) undertaken by the Environment Agency and devolved environment agencies under bathing water monitoring programmes (Palmer & Stapleton, 2023; Whelan et al., 2022), with simple ecological bioindicators, and an interaction risk matrix informed by local enrichment context and thermal extremes, so that improvements in spill reduction translate into demonstrable ecological recovery signals rather than solely anthropocentric health classifications.

Finally, Chapter 5 positions multiple stressor evidence within a rapidly evolving global governance landscape in which climate change, biodiversity, and ocean use are increasingly treated as coupled challenges. In parallel to expectations from the Convention on Biological Diversity (Convention on Biological Diversity, 2024; Reimer et al., 2020; Winther et al., 2020) and blue economy initiatives such as the European Ocean Pact (European Commission, 2025; High Level Panel for a Sustainable Ocean Economy, 2023; Knol-Kauffman et al., 2023), the BBNJ Agreement (High Seas Treaty) is becoming a major new institutional locus for translating science into protection and sustainable use in areas beyond national jurisdiction. The treaty has recently surpassed the 60-ratification threshold needed for entry into force, set to commence on 17 January 2026, coinciding with the submission of this thesis (Guterres, 2025; High Seas Alliance, 2025). The BBNJ framework explicitly elevates environmental impact assessment, area-based management tools, and capacity-building and technology transfer (United Nations, 2023); mechanisms through which interaction-aware evidence can be practically operationalised. Consequently, a key future direction is to ensure that the scientific evidence emphasised throughout this thesis, including clear interaction typologies, consideration of context moderators, biotically mediated pathways, and spatiotemporal variability, are designed from the outset to be legible and usable within these

emerging governance structures, ultimately to facilitate the swift uptake of multiple stressor science as a matter of implementable practice, rather than aspiration.

6.3 Conclusions

Coastal ecosystems currently experience intensifying climatic extremes against a suite of land-based pressures, accelerating ecological change and raising the stakes for timely, proportionate adaptation (IPCC, 2023). In this setting, the practical challenges for marine conservation and management include a clear lack of multiple stressor acknowledgement and evidence across the land–sea interface. Scientific evidence about multiple stressors is growing, yet stressor outcomes remain difficult to compare across studies and to incorporate into assessment and planning when scale, null expectations, and ecological meaning are not made explicit (Piggott et al., 2015; Schäfer & Piggott, 2018; Spake et al., 2023). Meanwhile, the policy demand for multiple stressor science continues to grow, often in contexts where uncertainty, data limitations, and capacity constraints shape what is feasible in decision-making (Hodgson & Halpern, 2019; Thyrring et al., 2025; Tolochko & Vadrot, 2021).

The central implication is that actionable multiple stressor science needs to prioritise decision-ready synthesis as much as academic detail. This includes empirical designs that are scalable and comparable across contexts, analytical approaches that communicate interaction outcomes transparently in relation to explicit null models, and intermediate products that are disseminated across the science–policy boundary, such as interaction typologies, timing-sensitive risk windows, and context moderators that inform where additive assumptions are most likely to be met or not (Duncan & Kefford, 2021; Lakens, 2017; Mack et al., 2022; Orr et al., 2020, 2024). Where management operates under partial control of stressors, such insights also help set interaction-aware expectations for evaluation, so that outcomes are interpreted against plausible joint dynamics rather than simplified assumptions about constancy or independence (Brown et al., 2013; Côté et al., 2016; Simmons et al., 2021).

This thesis contributes novel empirical and analytical evidence showing that multiple stressor effects are time-structured within seasons and across levels of biological organisation, and that stressor effects are heterogeneous across spatial scales. This thesis further demonstrates how that variability can be translated into more interpretable, decision-ready multiple stressor

logic for marine planning at the land–sea interface. The longer-term value, however, lies in the science-to-policy workflow it exemplifies: to pair distributed in situ evidence with scalable monitoring and data assimilation, to embed those signals into adaptive decision triggers, and to do so through equitable collaboration models that broaden who produces evidence, whose knowledge is included, and which risks and trade-offs are prioritised. In a marine governance landscape increasingly oriented toward cumulative effects, climate risk, and cross-sector coordination, this thesis demonstrates a practical route for collecting and translating multiple stressor evidence into implementable planning and management at the land–sea interface.

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