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Warming simplifies marine ecological networks through losses in trophic and non-trophic interactions

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ABSTRACT: Ocean warming is anticipated to push many marine species beyond their physiological limits, leading to shifts in community composition and ecological interactions. Coastal upwelling can provide temporary relief from heat stress but may also introduce challenges due to temporal hypoxia and acidification. As environmental extremes become more frequent and prolonged, understanding their impact on coastal ecosystems is critical. To examine how warming and upwelling influence trophic and non-trophic network complexity, we quantified trophic group biomasses and ecological network properties in benthic mesocosm communities. Over a 4.5 mo summer period, seawater temperatures were experimentally manipulated, ranging from ambient conditions to +5°C above ambient, and further crossed with transient upwelling events. The most striking result was that total biomass was about 50% lower in the warmest treatments compared to ambient conditions. *Fucus* spp. biomass was 50–76% lower in warmer treatments and entirely absent at +5°C. As a foundational species, *Fucus* loss led to a ~39% reduction in non-trophic interactions. Under extreme warming, predatory sea stars also disappeared. These shifts at both the base and top of the food web were associated with reduced connectance, omnivory, and generality in warmer treatments, as well as reductions in ecosystem functioning, such as community biomass and carnivorous fluxes, suggesting food web simplification with increasing temperature. By integrating experimental data with ecological network modelling, this study provides a holistic view of how coastal communities may respond to future climate change, highlighting the risks of coastal biodiversity loss on ecosystem functioning.

KEY WORDS: Ecosystem functioning · Foundation species · Long-term mesocosm experiment · Ocean warming · Ocean upwelling · Marine heatwaves · Multi-layer networks · Multiple stressors

1. INTRODUCTION

Ocean warming, in combination with marine heatwave (MHW) events — periods of anomalously warm temperatures lasting for days to several months (Hobday et al. 2016, Smith et al. 2025) — has already pushed coastal species beyond their tolerance limits (Straub et al. 2019, Estaque et al. 2023), with species loss and disruption of ecosystem functioning as a consequence (Smith et al. 2021). As such, ocean warming poses one of the most pervasive global threats to coastal biodiversity (Wernberg et al. 2024). Upwelling events may provide temporary relief from heat stress, yet the complex changes in abiotic conditions (nu-

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trient regime, oxygen levels, carbonate system) during upwelling events (Wahl et al. 2021) and their interactions with climate change-related stressors and associated impacts on ecosystems are not well understood (Joyce et al. 2024), especially for multitrophic communities (but see Polazzo et al. 2022, Gomes et al. 2024). Meanwhile, ecosystems are changing rapidly in the face of climate change. This calls for a holistic assessment of the impacts of multiple environmental stressors on species interactions in complex ecological communities to understand — and mitigate — the future risks to coastal ecosystems.

Ecological network analyses provide a means to study complex ecosystems and their response to environmental change (Kortsch et al. 2015). Ecological networks encompass a range of species interactions, including trophic interactions, mutualism, competition, amensalism, and commensalism (Bersier 2007). Among these, the most extensively described are trophic networks, or food webs (Delmas et al. 2019). Meanwhile, non-trophic interactions also play a crucial role in shaping species diversity and in defining co-existence (Ings et al. 2009, de Ruiter & Gaedke 2017, Miele et al. 2019), particularly in coastal communities, where foundation species, such as seaweeds and corals, provide refuge and habitat for other species (Ellison 2019). Generally, non-trophic interactions are underreported and seldom combined with food web analyses (but see Kéfi et al. 2012, Miele et al. 2019, Perälä et al. 2023, Salinas et al. 2023). Yet to comprehend the full range of changes in an ecological community, especially in coastal ecosystems, trophic and non-trophic interactions must be studied jointly.

Temperature has a profound impact on food web dynamics, primarily by influencing species metabolism (Brown et al. 2004). Under warming, consumers may face difficulties in meeting increased energy demands (O'Connor et al. 2009). This can result in constraints on growth, reproduction, or activity when species-specific temperature thresholds are exceeded (Wahl et al. 2020). At the food web level, this can potentially lead to shorter, simpler food webs (Fussmann et al. 2014, O'Gorman et al. 2019, Polazzo et al. 2023). It may also alter the distribution of biomass and interaction strengths across the food web (Nagelkerken et al. 2020), reduce efficiency in energy fluxes (Barneche et al. 2021), and even increase the risk of food web collapse (Ullah et al. 2018, Nagelkerken et al. 2020). MHWs may speed up this process and push food webs beyond their resilience with minimal time for species to acclimate and adapt (Gruber et al. 2021). This is particularly concerning when the impacts involve foundation species (Agostini et al. 2021). These play a crucial role in shaping and maintaining coastal ecosystem diversity through their abundance at the base of the food web and their many ecological interactions (Wernberg et al. 2024). Among these, non-trophic interactions in particular facilitate the existence and diversity of associated species, such as invertebrates and fish (Miele et al. 2019, Smith et al. 2023).

Whereas warming effects on food webs are well-studied, significant knowledge gaps remain regarding how other pressures interact with warming in shaping ecological network structure (Polazzo et al. 2022). Eastern boundary upwelling transports deep, cold, nutrient- and carbon-rich but low-pH and deoxygenated water to the surface ocean, often increasing overall biological productivity but with negative impacts on the calcification of species (Kroeker et al. 2023, George et al. 2024). The strength and direction of the effects of sporadic wind-driven upwelling events in the Baltic Sea are shifting seasonally, providing primary productivity through nutrient-rich waters in spring (Lehmann & Myrberg 2008), while acidified and hypoxic conditions can be detrimental to shallow coastal systems during late summer and early autumn (Melzner et al. 2013, Wahl et al. 2021). Meanwhile, upwelling of cooler waters can provide some stress relief from MHW conditions during peak summer (Wolf et al. 2022, Rühmkorff et al. 2023). Changes in the carbonate system and decreased oxygen can affect the survival or growth of species (Vaquer-Sunyer & Duarte 2008, Seibel 2011, Bednaršek et al. 2021), potentially shifting species dominance or community composition (Dabuleviciene et al. 2023) and associated trophic interactions. Nagelkerken et al. (2020) investigated the effects of warming and acidification on food webs, finding that food web architecture can be inflexible under ocean warming, leading to an inability to compensate for the decline of taxa and an increased risk of ecosystem collapse. Still, the combined and interactive effects of warming and natural upwelling events on coastal organisms are poorly understood, especially at the food web level.

In this study, we explore new approaches to integrating ecological network analysis with existing mesocosm data, simulating a future coastal ocean climate. Elements of this study are inherently explorative and descriptive, aiming to provide a conceptual perspective on the potential consequences of species and interaction losses from climate change. To do this, we analysed the impact of 6 warming scenarios, with and without upwelling events, on species community composition, using data from a 4.5 mo-long, close-to-natural mesocosm experiment in the Kiel Fjord, western

Baltic Sea (Wahl et al. 2021). The recorded temperatures in the 12 tanks represented a gradient of MHW intensities following the widely applied definition by Hobday et al. (2016) and using a 22 yr (1997–2018) baseline from the Kiel Fjord (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/meps15092_supp.pdf; Wolf et al. 2020). Our mesocosm community included multiple trophic groups (food web components), such as macrophytes, mesograzers, filter feeders, and predatory invertebrates. To comprehensively assess the dynamics of food web structure and function, we employed both unweighted (topology-based) and weighted (flux-based) food web approaches. Furthermore, we examined non-trophic interactions in the mesocosm communities, focusing on those closely connected to the foundation species *Fucus vesiculosus* and *F. serratus* (Wahl et al. 2011), hereafter *Fucus*. To uncover how warming, upwelling, and their interaction influence species community composition and ecological network structure, we addressed the following research question: How do biomasses of trophic groups, food web properties and functions, as well as non-trophic interactions vary with warming scenarios and upwelling events? We hypothesised that warming (1) increases the biomass of opportunistic primary producers, while reducing that of top consumers, with upwelling mitigating these effects by alleviating heat stress; (2) simplifies food web structure, manifested as a loss of trophic interactions and declines in network properties such as connectance and omnivory, with upwelling buffering these effects; and (3) causes a loss of non-trophic interactions and a reduction in functional complexity, particularly those associated with habitat-forming foundation species, while upwelling may help preserve them.

2. MATERIALS AND METHODS

2.1 Study site and experimental design

The experiment was conducted in the Kiel Outdoor Benthocosm (KOB) system in the Kiel Fjord, Germany (Western Baltic Sea), a mesocosm infrastructure comprising 12 independent 1500 l tanks. The KOBs are located on a float moored outside the GEOMAR Helmholtz Centre for Ocean Research Kiel (54.330216° N, 10.149815° E). In brief, the open (flow-through) system is equipped with computer-controlled heaters and chillers, regulated by an aquarium automation system (Profilux-3ex with Expansion Box and powerbars; GHL Advanced Technology), allowing for the maintenance of temperature offset levels. Temperature is continuously monitored using PT1000 platinum resistance thermometers, while internal circulation and wave generators simulate natural hydrodynamic conditions. For a detailed description of the KOB infrastructure, see Wahl et al. (2015).

The experiment ran for a total of 132 d (~4.5 mo) between 2 May and 11 September 2018. In brief, the mesocosm tanks were supplied with unfiltered through-flowing fjord water, and the entire water volume of each tank was replaced about 7 times per day. The experimental set-up represented a fully crossed multiple-driver approach (Boyd et al. 2018), here warming and upwelling, in a non-replicated multiple-regression design. For more information on the limitations of such approaches and the statistical analysis, see Sections 4.5 and 2.4. For a detailed description of the specificity of the current experiment, consult Wahl et al. (2021).

Six warming scenarios were implemented, ranging from naturally fluctuating, ambient fjord temperatures to +5°C above ambient (0–5°C in 1°C increments). A gradual increase in temperature was implemented to reach the target treatment levels from 2–12 May, with an acclimation rate of 0.5–1°C d^{-1}. The warming treatments covered the range of temperature increases projected to occur in the Baltic Sea by 2050–2200 (under the RCP8.5 scenario; Meier et al. 2022). In 2018, natural Kiel Fjord temperatures were characterised by considerable temperature fluctuations and 2 recorded naturally occurring MHWs encompassing a generally warm summer (Fig. S1). Details on the average, maximum and range of temperatures observed are presented in Table S1.

In half of the 12 tanks, the added warming of 0–5°C was interrupted by 3 simulated upwelling events (3–9 July, 4–11 August, and 28 August–3 September 2018; Figs. S1–S2) by switching to another water intake pipe at 14 m depth (i.e. below the thermocline) during the upwelling events. Surface water was replaced by upwelled water at a rate of approximately 7 tank volumes per day, recreating a gradual transition from surface to bottom conditions. The water supply rate remained constant throughout the experiment, independent of the water intake used. During these events, the temperature in each tank decreased by a consistent magnitude, although the absolute temperatures varied depending on the initial conditions. Temperature, salinity, pH, and oxygen levels were monitored throughout the experiment. Upwelled waters were cooler, poorer in oxygen, lower in pH, and more saline (Fig. S2), which is characteristic of upwelling events in the Kiel Fjord during the summer season (Wahl et al. 2021). These conditions led to

hypoxia (<2 mg O_2 l^{-1}), mainly during the third simulated upwelling event (Fig. S2). Notably, during the third simulated upwelling, a natural upwelling event occurred in the Kiel Fjord. As a result, even non-upwelling tanks receiving surface water showed transient drops in oxygen (Fig. S2).

2.2. Set-up and sampling of the mesocosm communities

At the start of the experiment, a benthic community representative of shallow coastal ecosystems in the area was reconstructed in each tank. Similar biomasses of the native brown algae *Fucus vesiculosus* (average 604 g, 3 individuals) and *F. serratus* (average 474 g, 3 individuals), along with their associated mesograzers (*Idotea balthica*, *Gammarus* spp.), at densities found on the algae at the time of sampling, as well as 20 individuals of *Littorina littorea* and 10 individuals of *Mytilus edulis*, were added to the tanks (Tables S2 & S3). Due to a later start in their growth season, fronds of the non-indigenous red alga *Gracilaria vermiculophylla* (100 g per tank) were distributed into the tanks 50 d into the experiment (Wahl et al. 2021). The mesocosm community was largely untouched during the experiment, with only minor biomasses of *Fucus* or *G. vermiculophylla* being removed or added for macroalgae performance measurements and interaction with grazers (Table S3). As the inflowing water to the tanks was not filtered, natural recruitment of filter feeders and mesograzers occurred over the course of the experiment. Epiphytic algae were kept untouched throughout the experiment.

As substrate for the natural recruitment of soft-bottom fauna during the experiment, plastic containers (17 × 25 cm) filled with sieved (1 mm) and homogenised sand were placed at the bottom of each tank. For the recruitment of hard-bottom fauna and flora, settlement panels (PVC, 12 × 12 cm, inclined at 30°) were hung from the side wall of each tank (Tables S2 & S3).

At the end of the experiment, the mesocosms were sampled for abundance and biomass data for all species within the tanks. Species with fewer than 3 individuals across all samples were excluded (Fig. S3). Diverse sampling methods were employed for the different components of the experimental tanks (detailed in Table S2). In brief, predators were weighed directly, macroalgae were cleaned and weighed for biomass, and sediment was sieved to collect soft-bottom fauna. Organisms in the water column and *Fucus* community were sampled using nets, while fouling organisms on PVC panels were quantified based on percentage cover. Using certain methods, only abundance data were recorded (Table S2). In these cases, we estimated average biomasses for species using either quantified average body masses for conspecifics present in other parts of the tanks or by consulting available literature on average body masses of these species (see Text S1 & Table S4). For a more comparable estimate of the final community at the tank level, biomass estimates of species from the different tank components were scaled (see Text S1 & Table S2). All species in the mesocosms were identified to the lowest possible taxonomic level (genus or species), except for microphytobenthos, phytoplankton, and detritus, which were kept as 3 separate basal nodes of the food web.

2.3. Construction of ecological networks

Trophic interactions were compiled through an extensive literature search of existing databases and diet studies from the Baltic Sea (Table 1, Fig. 1a), following a similar approach to Olivier et al. (2024) and expanding on previous work (Kortsch et al. 2021, Olivier et al. 2024). It is common practice to construct food web studies using literature data (Delmas et al. 2019), which capture 'potential' rather than 'realised' trophic interactions among species. Accordingly, our approach describes the 'potential loss' of trophic interactions, whether through species loss or gain (shifts in community composition) in response to environmental stressors, rather than realised losses. Despite a thorough review, a few taxa (8%) lacked sufficient diet information. In these cases, we inferred trophic links by assuming that closely related species (e.g. within the same genus or family) share similar predators and prey (Olivier et al. 2019). The final trophic interaction list underwent verification in consultation with experts at GEOMAR Kiel, Germany. The metaweb (Fig. 1) is available with references on Zenodo https://doi.org/10.5281/zenodo.17802760.

To avoid complete predation of benthic invertebrates recruiting in the mesocosms, the 2 top predators — the common sea star *Asterias rubens* and the green shore crab *Carcinus maenas* — were housed in separate compartments within the mesocosms. Three individuals of each species were collected (crabs on 11 June and sea stars on 18 June from Kiel Fjord) and added to the experiment on 18 June, each individual in its own compartment (i.e. 3 compartments per species). Consequently, their role and impact in the food web analyses only reflect their potential interactions and

Table 1. Selected food web metrics examined and their definitions

Food web metric	Definition	Implications (ecological or structural)
Species number (S)	Number of tropho-species (nodes) in the food web	Species richness is an indicator of diversity
Number of links (L)	Number of links in the food web	Informs on the number of species interactions and connectivity of the food web
Connectance (C)	Proportion of realized links in a network	Indicates how well-connected the food web is and has implications for stability
Generality (G)	Average number of prey per predator	Indicates whether the food web has more generalists or specialists
Level of Omnivory (Omni)	The standard deviation of the trophic level of a species resources	Describes the diet width across trophic levels and influences stability
Mean trophic level (TL)	The average trophic level is calculated as the sum of each species' longest trophic level divided by the total number of species. The longest trophic level represents the maximum number of steps between a given consumer and a basal species	Describes the vertical structure of the food web by indicating the average trophic position of species in the food web
Carnivory (Carni)	Total energy flux through predatory (carnivorous) interactions in the food web, expressed as kJ m^{-2} d^{-1}	Shows to what extent the network contains predatory energy fluxes
Herbivory (Herbi)	Total energy flux through herbivorous interactions in the food web, expressed as kJ m^{-2} d^{-1}	Shows to what extent the network contains herbivorous energy fluxes

energy flows, not their realised ones. Yet predators can influence the invertebrates by inducing behavioural responses (e.g. predator avoidance) through waterborne cues (e.g. Leonard et al. 1999, Hay 2009).

Beyond feeding relationships, non-trophic interactions are crucial in shaping coastal community structure and dynamics (Bruno et al. 2003). To examine how these interactions shift in response to warming and upwelling, we mapped non-trophic interactions among species pairs (Fig. 1), categorising them as interference competition (−/−), exploitative competition (−/−), antagonism (−/+), amensalism (−/0), commensalism (+/0), or mutualism (+/+). Interactions were based on an extensive literature search, local expert knowledge, and personal observations. This included reviewing studies that describe ecological relationships such as competition, mutualism, and commensalism, particularly in the Baltic Sea. Exploitative competition was inferred from the food web by identifying species sharing prey items, and, therefore, potentially competing for the same food resources. Competition among consumers feeding on 'microphytobenthos', 'detritus', and 'phytoplankton' was excluded, assuming no limitation of these resources in the tanks. As with trophic links, our aim was to capture ecologically plausible interactions rather than exhaustively document all possible relationships. Our list of non-trophic interactions is available with references at Zenodo (https://doi.org/10.5281/zenodo.17802760).

To estimate food web functions, such as changes in carnivorous and herbivorous fluxes, we assigned energy fluxes to the trophic interactions using a bioenergetic model. This approach is based on allometric scaling relationships between metabolism, body mass, and temperature (Brown et al. 2004). It assumes a steady state, implying that energy lost by a species through predation and metabolic processes is balanced by the metabolised energy gained from consumption (Barnes et al. 2018, Gauzens et al. 2019, Jochum et al. 2021). For more details on the bioenergetic model and model parameterisation, see Text S1. Energy fluxes were calculated using the 'fluxweb' R package (Gauzens et al. 2019), and the food web metrics were calculated using a custom-written code (available via Zenodo at https://doi.org/10.5281/zenodo.17802760). The R package 'igraph' (Csárdi & Nepusz 2006) was used to create the trophic as well as the non-trophic network graphs.

2.4. Numerical and statistical analyses

All data analyses were conducted in R (v4.3.1; R Core team 2023) using RStudio (Posit team 2023). To

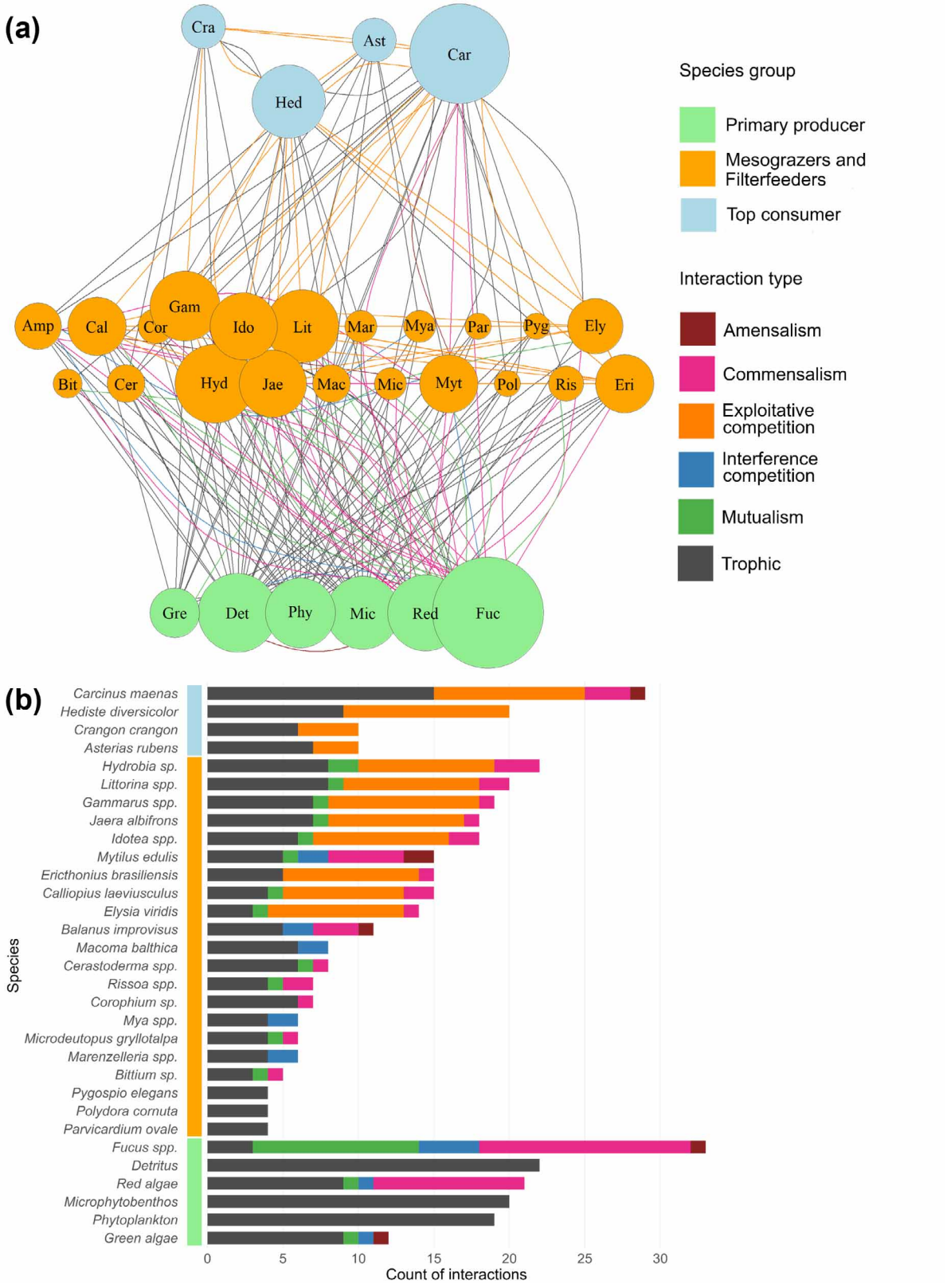

Fig. 1. (a) Metaweb of trophic and non-trophic interactions for the coastal Kiel Fjord (Baltic Sea) mesocosm community (see colour code of interaction types in the key). Node sizes are proportional to a taxon's total number of potential interactions (see colour code in the legend for species functional grouping). The metawebs consist of 29 nodes and 215 interactions in total, out of which 113 are trophic, 14 are mutualistic, 58 are competitive (50 for resources and 8 for space or substrate), 27 are commensalistic, and 3 are amensalistic. (b) Number and type of interactions (trophic and non-trophic) for each taxon, including both in- and outdegree (i.e. incoming and outgoing interactions)

assess how food web structure and functions varied across the warming scenarios and the upwelling events, we quantified 7 unweighted, topological and 2 weighted, flux-based network properties: herbivory and carnivory. The topological properties, which consider presence—absence of nodes and interactions only, include number of species (S), number of trophic links (L), connectance (C), mean generality (G), mean trophic level (TL), and mean level of omnivory (Omni; Table 1). The flux-based network properties were calculated using the 'fluxweb' R package (Gauzens et al. 2019), based on species biomasses, metabolic rates and allometric scaling laws. Herbivory was defined as energy flux from basal resources (including detritus), and carnivory as flux from consumer species. The number of non-trophic links was quantified to assess how non-trophic network structure varied across warming and upwelling scenarios and was included in both the multivariate and statistical analyses.

To analyse the relationships between biomass changes, food web metrics, and treatments (i.e. warming scenarios and upwelling events), we applied generalized additive models (GAMs). While replication is essential for estimating within-treatment variability in categorical designs, our study followed a gradient-regression approach where temperature is treated as a continuous covariate. This design prioritises resolution across the gradient over replication at discrete levels, enabling the detection of nonlinear trends using GAMs. This approach is consistent with ecological modelling practices that advocate for gradient-based designs to better capture environmental variability (Cottingham et al. 2005, Kreyling et al. 2018, Marshall 2024). Moreover, GAMs have been successfully applied to similar gradient-based mesocosm experiments (Ersoy et al. 2022, Moffett et al. 2023). We used the 'gam' function from the R package 'mgcv' (Wood 2017), which allows for the flexible modelling of non-linear relationships using smooth functions. Three sets of GAM models were fitted for each biomass or metric, each with different combinations of predictors and error distributions. Each model includes smooth terms (denoted s() in GAMs) for warming and warming by upwelling interactions, allowing for different responses to warming at each upwelling level, or only s(warming) and upwelling, or only s(warming). Model selection was based on Akaike's information criterion (AIC), and the model with the lowest AIC was selected as the best-fitting model (Tables S5 & S6 in the Supplement). Specifics about the fitted models, including diagnostics, their random effects, link functions, smooth terms, and error distributions, are provided in Text S1, Tables S7 & S8 and Figs. S4 & S5. Furthermore, to examine the most important associations among the food web metrics and functions, as well as warming and upwelling treatments, we applied a principal component analysis (PCA) to explore and summarise variation in food web metrics across treatments using the R package 'factoextra' (Kassambara & Mundt 2020).

3. RESULTS

3.1. Changes in biomass

Biomass across all mesocosm tanks was dominated by primary producers, accounting for 78—91% of the total biomass (Figs. 2a,b), whereas mesograzers and filter feeders (shell-free dry weight) accounted for 4—16% of the biomass (Figs. 2c,d). Overall, biomasses of the different trophic groups showed an almost linear decrease across the warming gradient, with a less pronounced effect of upwelling events (Fig. 2; Table S7).

To test for relationships among treatments and response variables, we conducted GAMs, in which 'high deviance explained' reflects a good model fit (Wood 2017). Total biomass (sum of all trophic groups) was progressively lower with increased warming, dropping from about 600 g in the +0°C treatment to roughly one-third in the warmest treatment without upwelling, to almost zero when upwelling was applied (Fig. 2f). This pattern was statistically significant ($p < 0.001$), with the GAM accounting for 87.8% of the deviance explained (Table S7).

The biomass of the foundation species (*Fucus*) was significantly lower in the warmer treatments ($p < 0.001$), whereas upwelling had no significant effect (Fig. 2a; Table S7). The GAM accounted for 87.7% of the deviance explained in foundation species biomass (Table S7). *Fucus* biomass was reduced by 50% in the +2 and +3°C treatments and collapsed under +5°C warming (Fig. 2a). The biomass of green and red filamentous algae (other primary producers) was significantly higher with warming ($p < 0.001$) and showed a significant negative effect of upwelling ($p < 0.001$; Fig. 2b; Table S7). The increase in filamentous algal biomass was much steeper in treatments without upwelling, tripling in the +5°C scenario (Fig. 2b). The GAM accounted for 61.5% of the deviance explained (Table S7). In warming scenarios of +3°C and beyond, mesograzer biomass was halved compared to ambient conditions (Fig. 2c). The reduction in biomass was significant ($p < 0.001$), with the GAM accounting for 90.5% of the deviance explained (see Table S7). Both filter feeders and top consumers exhibited similar

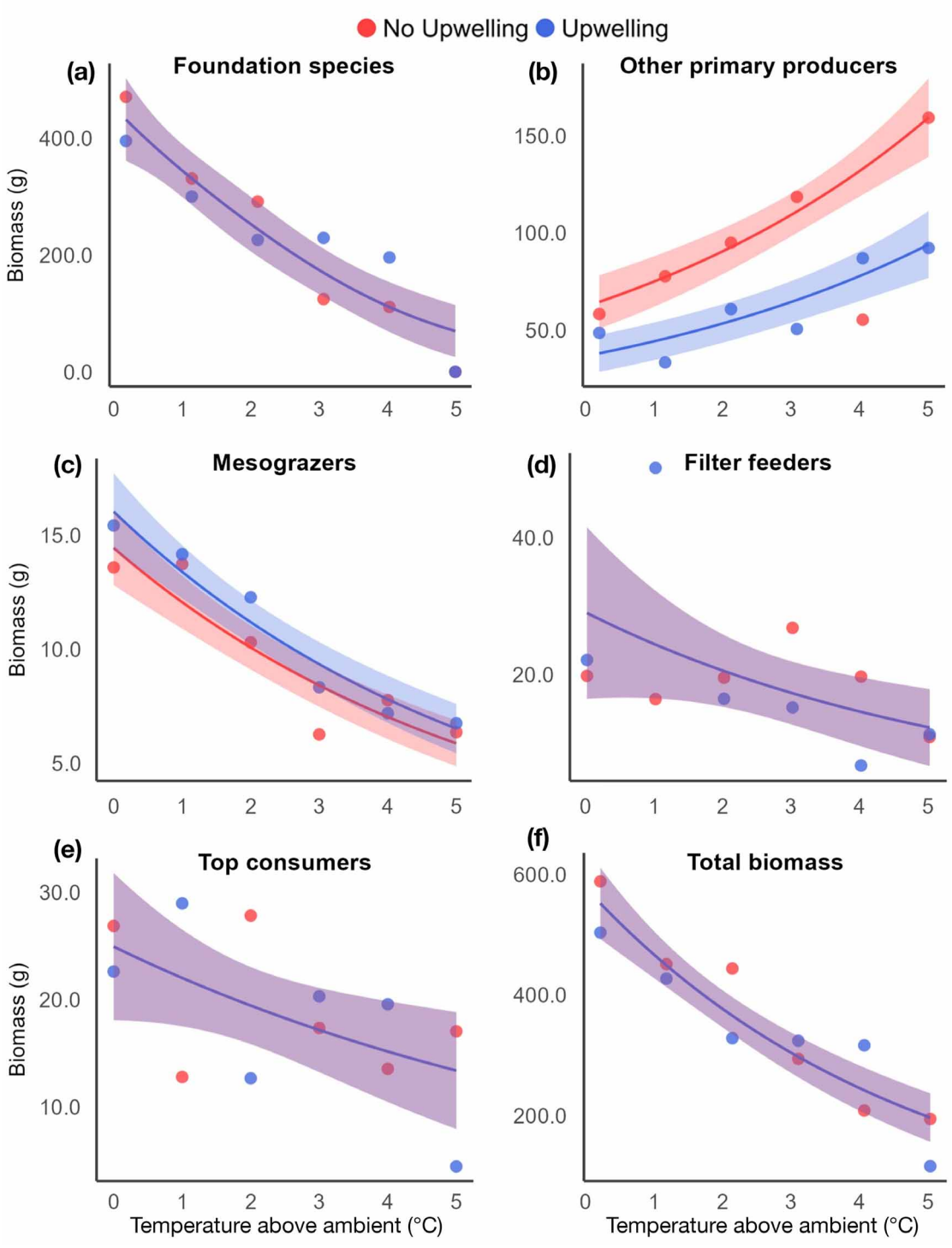

Fig. 2. Variation in total biomass of different trophic groups in response to warming scenarios and upwelling events. Species groups are categorised as follows: (a) foundation species: *Fucus vesiculosus* and *F. serratus*; (b) other primary producers: microphytobenthos, phytoplankton detritus, green and red algae; (c) mesograzers: isopods, amphipods, polychaetes, and gastropods (15 species in total); (d) filter feeders: *Balanus improvisus*, *Cerastoderma* spp., *Macoma balthica*, *Parvicardium ovale*, *Mya arenaria*, and *Mytilus edulis*; (e) top consumers: *Crangon crangon*, *Asterias rubens*, *Carcinus maenas*, and *Hediste diversicolor*; and (f) total biomass, which includes all trophic groups. Trends were modelled using generalized additive models. Dots: biomass values; shaded areas: 95% confidence intervals. For data with non-significant upwelling effects (a, d, e, f, following AIC benefitting the most parsimonious model), the data was pooled. Detailed statistical results are given in Table S7

reductions in biomass in response to the warming scenarios (Fig. 2d,e), albeit with a less steep slope and higher variability between tanks compared to biomass changes of the other trophic groups (Fig. 2).

3.2. Changes in food web metrics and functions, and in non-trophic interactions

Out of the 215 links in the metaweb, 102 were non-trophic interactions (Fig. 1). Of these, 57% were competitive, mostly involving mesograzers or top consumers, whereas 40% were facilitative. Most of the positive non-trophic interactions (commensalism and mutualism) arose through the structure of habitat-forming macrophytes. Among herbivore species, the snails *Hydrobia* spp. and *Littorina* spp. were prominent, with most of their links being competitive non-trophic links (Fig. 1). Among the top consumers, the crab *Carcinus maenas* and the polychaete *Hediste diversicolor* had the highest numbers of non-trophic links, mainly competitive interactions for prey items shared with other consumers.

Unweighted and weighted food web metrics varied across the warming scenarios, with the number of trophic links being 10–15% lower in the warmer treatments compared to ambient (Fig. 3). The number of non-trophic interactions was 36–39% lower in the warmer scenarios (Fig. 3). Exploitative competition was the most frequent type of non-trophic interaction across the warming scenarios, while commensalistic links in the +0 to +4°C networks were also common, but were notably less frequent at +5°C (Table S9). In the warmest scenarios, the absence of *Fucus* corresponded to 38–39% fewer non-trophic interactions (Fig. 3; Table S9), as it had the highest number of such links (n = 34).

According to the applied GAMs, the number of trophic links and carnivory were significantly lower (Fig. 4b,h) with increasing warming ($p = 0.042$ and $p = 0.011$, respectively) and accounted for 35.3 and 61.5% of the deviance explained, respectively (Table S8). For connectance, there was a significant interaction between warming and upwelling ($p = 0.044$). Here, the upwelling treatments showed a parabolic response curve across the 6 warming scenarios, with optima between the 2 and 3°C warming scenarios, followed by a steep drop in this metric (Fig. 4c). In the +5°C upwelling treatment, there was a sudden drop in generality (Fig. 4d) due to the loss of the predatory crab *C. maenas*, the species with the highest number of trophic links in the food web. The GAMs accounted for 66.3 and 84.1% of the deviance explained for connectance and generality, respectively (Table S8). A similar pattern of parabolic response was also observed for omnivory, increasing with increasing warming ($p = 0.015$; 64.8% of the deviance explained), but irrespective of upwelling (Table S8). Here, optima appeared between the 2 and 3°C warming scenarios (Fig. 4f). Interestingly, herbivory showed a significant upwelling effect ($p = 0.015$), while the warming effect and the interaction of warming and upwelling were not significant (Table S8). The 2 GAMs retrieved show deviating trends over the warming scenarios, with a decrease in herbivory seen in the upwelling treatments and an increase without upwelling (Fig. 4g). The GAM accounted for 37.9% of the deviance explained only (Table S8). For details on all warming scenarios and trophic and non-trophic networks, see Figs. S1, S6–S8.

3.3. Associations between food web structure and function, non-trophic interactions, and warming scenarios and upwelling

To identify which food web metrics and functions account for most of the variation across treatments, we applied a PCA. The first 2 principal components (PC1 and PC2) accounted for 72.8% of the total variability in the data (Fig. 5), of which PC1 and PC2 accounted for 39.8 and 33%, respectively. Warming was the driver most strongly associated with PC1, and hence explained most of the variability in the data. The food web metrics most strongly correlated (all negatively) with PC1 were the number of trophic links, the number of non-trophic links, the number of species, and mean trophic level, implying that these metrics are lower in warmer treatments. The metrics correlated (also negatively) with PC2 were connectance, omnivory, and generality (Fig. 5). The warming scenarios encompassing upwelling presented more negative PC1 scores than the ones without upwelling. Based on network structure, the 3 cooler scenarios (0 to +2°C) demonstrated greater similarity, clustering on the left side of the PCA. The 3 warmer scenarios (+3 to 5°C) showed higher variability in network structure, mostly captured by PC2.

4. DISCUSSION

Our mesocosm experiment on coastal communities exposed to warming scenarios under both non-upwelling and upwelling conditions revealed significant responses at the food web level. One of the most striking findings was a 50% reduction in total biomass

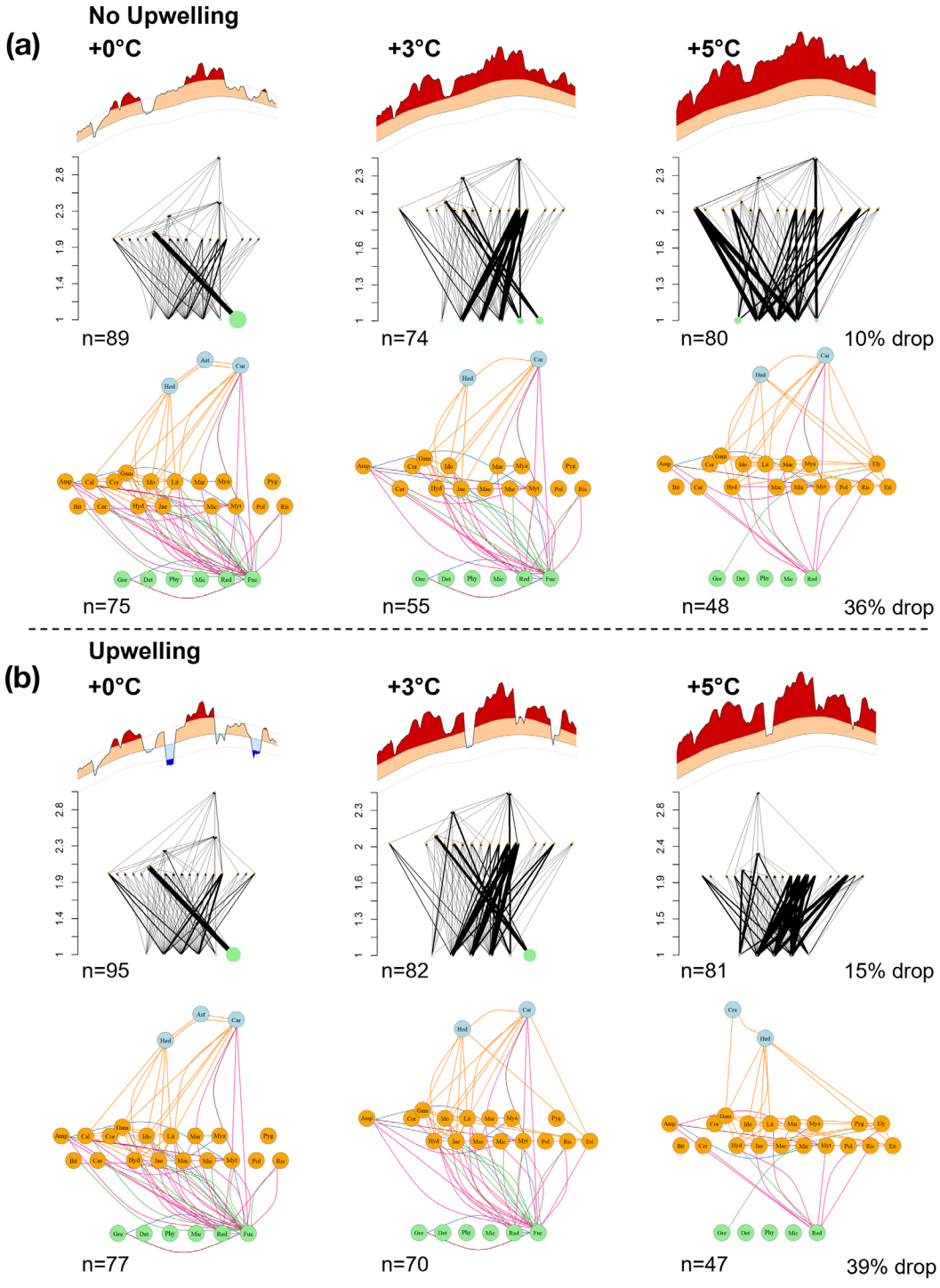

Fig. 3. Temperature curves (upper rows), flux-weighted food webs (middle rows), and non-trophic networks (lower rows) for 3 of 6 selected warming scenarios (+0, +3, and +5°C, left to right) for (a) no upwelling and (b) upwelling treatments. Curves are presented in relation to an existing background climatology modelled after Hobday et al. (2016), using a 22 yr temperature dataset from the Kiel Fjord; red indicates periods of marine heatwaves. The flux-weighted food web structures are presented as a response to warming scenarios and upwelling events, each node representing a species, with node sizes representing its total biomass. Line thickness is proportional to energy flux. Total number of links (L) is displayed to the left of the food webs (n); the number of links drops 10–13% from the ambient (+0°C) to the highest warming scenario (+5°C). Non-trophic networks show competitive (interference and exploitative), commensalistic, mutualistic, and amensalistic links. Total number of non-trophic links is displayed to the left of the non-trophic webs; number of non-trophic links drops 36–39% from the ambient to the highest warming scenario. For colour code, see Fig. 1. For details on warming scenarios and trophic and non-trophic networks, see Figs. S1, S6–S8

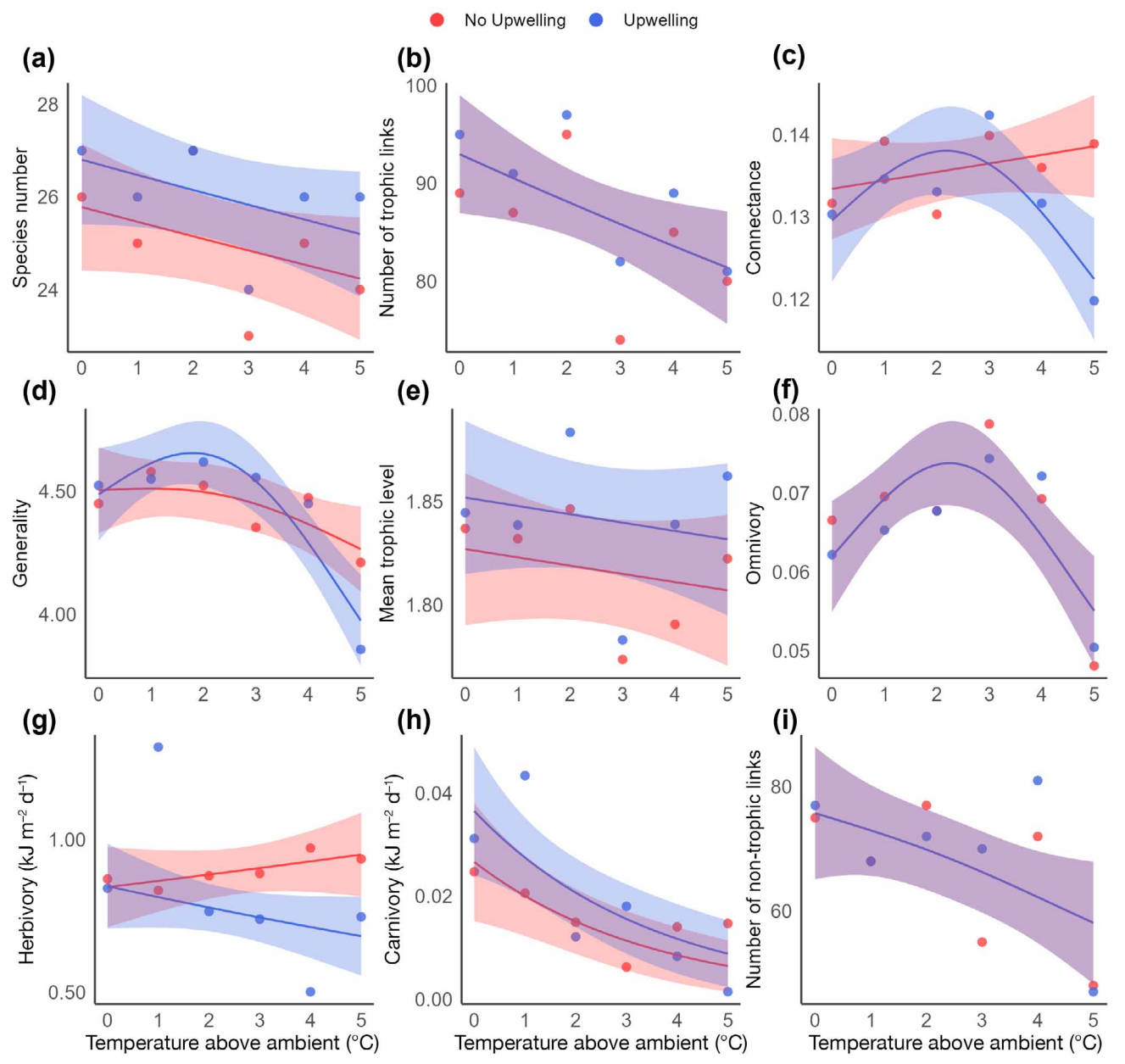

Fig. 4. (a) Unweighted network metrics species number, (b) number of trophic links, (c) connectance, (d) generality, (e) mean trophic level, level of omnivory, and median network fluxes (kJ m^{-2} d^{-1}) for (f) omnivory, (g) herbivory, and (h) carnivory, as well as the (i) number of non-trophic links in response to the warming scenarios and upwelling events. For descriptions of the metrics and functions, see Table 1. Trends were modelled using generalized additive models. Shaded areas: 95% confidence intervals. For data with non-significant upwelling effects (b; following AIC benefitting the most parsimonious model), the data was pooled. Detailed statistical results are given in Table S6

across the warming gradient, consistent with expectations from *in situ* measurements (O'Connor et al. 2009, Smale et al. 2013). Notably, the primary producer *Fucus* biomass was 50–76% lower in the warmer treatments and was entirely absent under the most extreme +5°C scenario. This led to a substantial ~36% reduction in non-trophic interactions, particularly because facilitative interactions (mutualism and commensalism) were less frequent. Species loss was also observed at higher trophic levels, with the disappearance of the sea star *Asterias rubens* in warming treatment above +1 and +2°C for no upwelling and upwelling, respectively (Wolf et al. 2022, Rühmkorff et al. 2023). Together, the loss of species and their trophic and non-trophic interactions at the bottom and the top of the food web, as well as the decreased total community

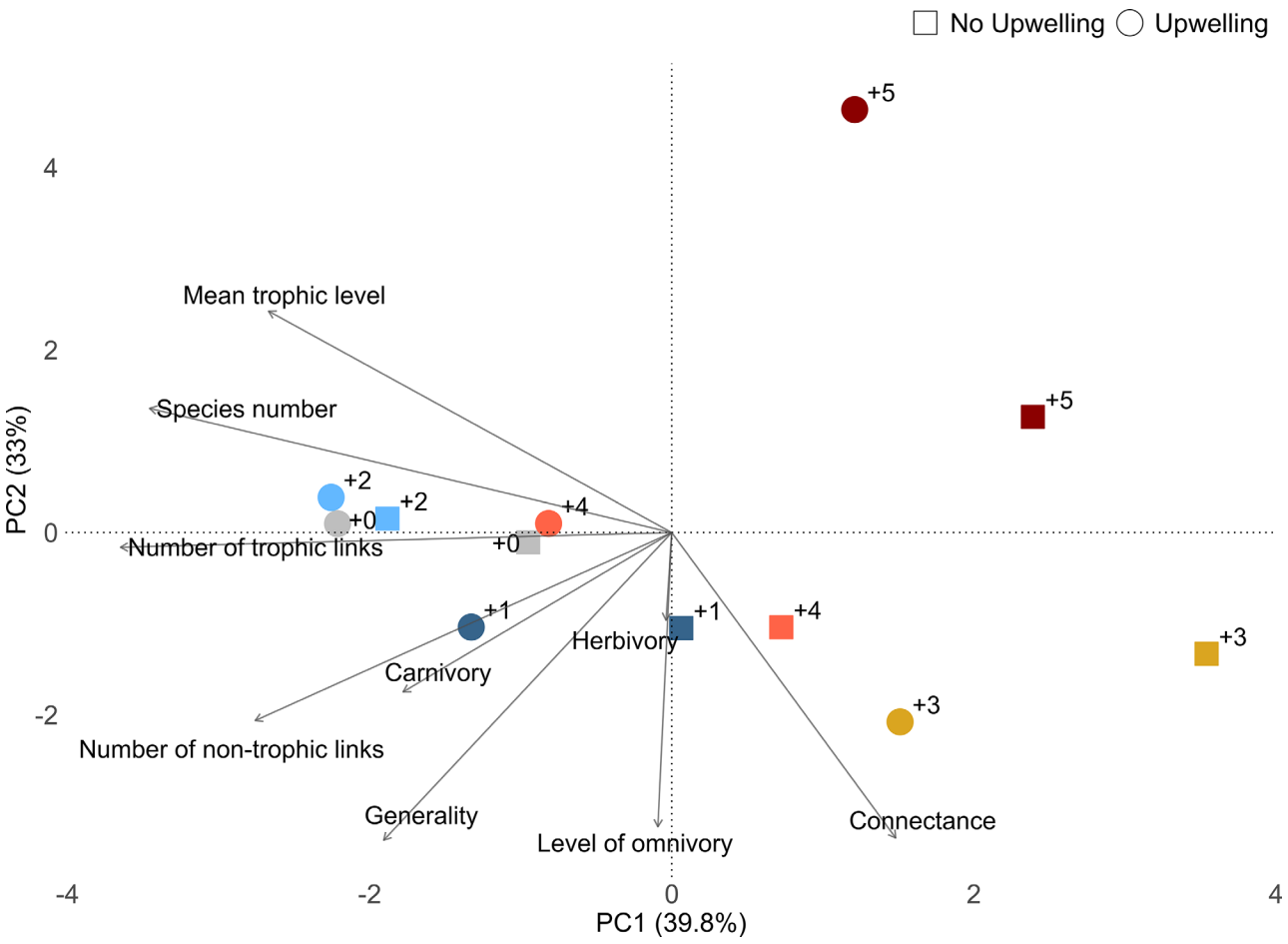

Fig. 5. Principal Component Analysis (PCA) biplot of the 6 trophic metrics (species number, number of trophic links, connectance, generality, mean trophic level, and level of omnivory), one non-trophic metric (number of non-trophic links) and 2 functions (herbivory and carnivory) summarising the dynamics in response to the warming scenarios and upwelling events. Colours are set according to the warming level in each warming scenario

biomass, resulted in reduced food web complexity and ecosystem functioning with warming.

4.1. Warming drives changes in food web structure and function

Between upwelling and temperature treatments, warming was the main driver of changes in benthic food web structure, as indicated by PC1 (Fig. 5). The 3 lowest warming scenarios (+0–2°C) demonstrated greater similarity in network metrics, whereas the warmest treatment levels showed higher variability along both PC1 and PC2, which could indicate that the ecological network structure becomes more variable and unstable with increasing heat (Dakos et al. 2015, Gladstone-Gallagher et al. 2023). The most prominent shifts with warming were lower values in key food web metrics such as the level of connectance, omnivory, generality, and carnivorous fluxes. These findings align with theoretical (Petchey et al. 2010) and empirical (O'Gorman et al. 2019, Polazzo et al. 2023) work showing fewer trophic interactions as well as lower generality and connectance with warming. In our study, the lower values in metrics such as generality can be attributed to the loss of higher-level consumers, e.g. sea stars. This can potentially reshape benthic communities, as these species mediate community diversity and food web complexity (Paine 1966, White et al. 2020). However, the effects on stability by consumer losses can be species-specific (White et al. 2020), i.e. both stabilising and destabilising, and also depend on the stability dimension (e.g. temporal stability, resistance, resilience, and recovery) investigated (White et al. 2020, Polazzo et al. 2023). Therefore, disentangling how losses of

higher-level consumers trigger alterations in food web stability would require dedicated perturbation experiments.

Contrary to the findings by Wahl et al. (2021), we did not see clear mitigation effects provided by the upwelling events on community structure and function. One reason for this discrepancy may be the aggregation of species biomasses into trophic groups (e.g. mesograzers, filter feeders, or top consumers), which can mask opposing species-specific responses. For example, the sea star *A. rubens* survived slightly further along the warming gradient in treatments with upwelling (up to +2°C), compared to those without upwelling (up to +1°C). *Carcinus maenas* survived all treatments except +5°C with upwelling. These species-specific responses of top consumers emphasise the importance of examining treatment effects at the individual species level. This also indicates that aggregating species into broader groups, such as is commonly done in food web analyses or at higher organisational levels, may obscure important species-specific responses to environmental pressures. While broad trends in community structure and function, like overall lower biomass, can still be detected, the nuanced responses of individual species might be overlooked. Such species-specific dynamics make generalisation and prediction more challenging (White et al. 2020).

The biomass of ephemeral and opportunistic primary producers (green and red algae) was higher at higher temperatures, as expected based on empirical studies (Nagelkerken et al. 2020). However, this increase was somewhat compromised by the occurrence of upwelling events. This is in contrast to expectations, as the increased nutrient influx following the upwelling generally should promote growth of opportunistic algae (Takolander et al. 2017a). Similarly, although less pronounced, herbivory increased with increasing temperature, while it decreased over the warming gradient under upwelling. This could indicate a negative additive impact from upwelling on certain food web functions.

4.2. Lower biomass in warming conditions

The reductions in the biomasses for all trophic groups with warming are consistent with observations from experimental studies (O'Connor et al. 2009), indicating a decrease in general system productivity with warming intensity, likely due to increased mortality from physiological (e.g. energetic) constraints. The largest reductions in biomass were found for the seaweed *Fucus*, which constitutes the most important habitat-forming macroalgal species in the Baltic Sea (Barboza et al. 2019). In contrast, filamentous green macroalgae are strongly favoured by warming as well as other climate-change-related shifts in the environment (Takolander et al. 2017a) and could be expected to benefit from available space and reduced competition with *Fucus*. This suggests a potential warming-driven shift toward a community dominated by filamentous macroalgae and new benthic invertebrate grazers (Kraufvelin & Salovius 2004). For instance, the solar-powered seaslug *Elysia viridis* appeared in warmer treatments, likely in response to an increase in its preferred resource, the filamentous alga *Cladophora rupestris*.

Similarly, Nagelkerken et al. (2020) found decreases in macroalgae with warming and an increase in turf algal biomass in a mesocosm experiment. The observed shift in macroalgal composition aligns with a broader understanding of how coastal species respond to warming and MHWs (Wernberg et al. 2016, Smale et al. 2019, Smith et al. 2024), which can have substantial consequences for the ecological services provided by foundation species to associated fauna (invertebrates and fish), resulting in habitat simplification (Agostini et al. 2021) and declining diversity and abundance (Wernberg et al. 2016, Ellison 2019, Salo et al. 2023), with implications for trophic interactions (this study). Reductions in primary producers can disrupt food web functioning (Ullah et al. 2018), as less biomass at the bottom of the web will be available to sustain higher trophic levels that, in turn, require more energy due to warming-induced increases in metabolism (Brown et al. 2004).

4.3. Fewer non-trophic interactions following the loss of foundation species

The loss of a species not only results in its disappearance but also in the loss of its ecological interactions. These biotic effects can be more subtle and difficult to detect than direct physiological effects (Strona 2022). To assess these changes, we structured our experimental communities into trophic and non-trophic networks. Our findings suggest that coastal benthic communities in the Baltic Sea could lose up to 15% of their trophic and 39% of their non-trophic interactions if average temperatures rise by 5°C above current levels or if extreme heatwaves occur during peak summer. These losses stem from changes in both vertical and horizontal diversity, particularly at the top and bottom of the food web.

The lower number of non-trophic interactions across temperature treatments is mainly linked to the loss of *Fucus*, a foundation species in Baltic Sea coastal communities (Kautsky et al. 1992, Wahl et al. 2011). *Fucus* supports high macrofaunal diversity and biomass, including small invertebrates, crustaceans, juvenile fish, and foraging fish species (Kautsky et al. 1992, Wikström & Kautsky 2007, Rinne et al. 2022). Its reduced biomass is likely to further impact the distribution and abundance of associated species due to reduced habitat availability and food resources (Wikström & Kautsky 2007, Duarte et al. 2015). The loss of *Fucus*-associated trophic and non-trophic interactions could disrupt predator–prey dynamics and intensify competition among sessile benthic species. The observed lower mesograzer biomass during our experiments may be attributed to the loss of *Fucus* as a habitat and as an indirect food source, as it facilitates the growth of epiphytes and biofilms that grazers rely on (Korpinen et al. 2008, Takolander et al. 2017a).

The broader consequences of altered ecological interactions in *Fucus* communities remain difficult to quantify without a dynamic multi-species model or an experiment specifically designed to test these relationships. For instance, a dynamic trophic network model of a Chilean coastal food web showed that species losses had stronger effects on community biomass when non-trophic interactions were included compared to models focusing only on feeding interactions (Miele et al. 2019). This highlights the need for further research to disentangle the role of trophic and non-trophic interactions in ecosystem functioning under global change. A critical step toward this goal is improving the reporting and resolution of non-trophic interactions in ecological network analyses, which are often overlooked (but see Kéfi et al. 2015, Miele et al. 2019, Salinas et al. 2023). Our study, although mainly descriptive and qualitative, represents a crucial step towards this integration.

4.4. Implications for the investigated ecosystem

The Baltic Sea is currently experiencing rapid warming compared to many other seas (Belkin 2009, Reusch et al. 2018, Meier & Saraiva 2020), arguably making it prone to prolonged and more frequent heat stress experienced by prevailing ecosystems (Goebeler et al. 2022, Bashiri et al. 2024). Temperatures in the Western Baltic Sea Kiel Fjord range between 0 and 24°C throughout the year (Wolf et al. 2020), and in the summer, strong winds may induce the upwelling of deep water into Baltic coastal ecosystems (Lehmann & Myrberg 2008). The imposed warming scenarios and upwelling events, therefore, represent plausible scenarios in the coming decades. While the more intense scenarios from our experiment may appear distant, the Baltic Sea is already experiencing extreme temperatures relative to long-term climatology (Meier et al. 2022, Pinto et al. preprint https://www.researchsquare.com/article/rs-3910435/v1)), with likely lasting impacts on coastal ecosystems.

By the end of the 21st century, *Fucus*, the only widely distributed canopy-forming macroalga on hard substrates in the Baltic Sea, is projected to decline by 30% in its distribution (Jonsson et al. 2018). Our study indicates that in the absence of foundation species such as *Fucus*, coastal Baltic Sea habitats and food webs may simplify, resulting in reduced community diversity and increased dominance of filamentous green algae on rocky substrates (Takolander et al. 2017b). This would diminish key ecosystem services, including nutrient uptake, carbon sequestration, food availability, and habitat for associated marine organisms (Jonsson et al. 2018). The decline and disappearance of foundation species and key benthic top consumers have the potential to induce cascading effects through losses of species and their trophic and non-trophic interactions, both at the bottom and at the top of the food webs. Such disruptions can compromise the robustness and resilience of coastal ecosystems, making them less capable of recovering from future disturbances such as heatwaves (Mougi & Kondoh 2016, Ellison 2019), increasing the risk of regime shifts or long-term degradation.

4.5. Caveats and future directions

Our approach of retrieving heatwave characteristics from the implemented warming scenarios is solely empirical, ignoring thermal performance functions and thresholds of the species and their different life history stages and traits within the ecosystem (Wahl et al. 2020). Yet it provides valuable context, assuming species (and ecosystems) to be adapted to seasonally shifting temperatures within a particular range (climatological boundaries: 10th to 90th percentiles; Hobday et al. 2016). The warming and upwelling effects recorded, however, represent a sum of multiple stress effects, and our approach still lacks the capability of determining the cause for collapse, whether it be the constant exposure to stressful temperatures, the temporal exceedance of thermal limits, or both. Thus, mechanistic small-scale mesocosm and

laboratory studies will be crucial in complementing large-scale community-level mesocosm approaches.

To upscale the information from mesocosm experiments to food webs, we made several simplifying assumptions, which should be reconsidered in future efforts to integrate mesocosm experiments with food web modelling. Two key assumptions were that (1) species interact if previously documented to do so, and (2) consumers prefer their most abundant prey. Consequently, the extent to which the interactions in our mesocosm food webs were realised, and the strength of these interactions in terms of energy flow, remains uncertain. Therefore, our study cannot address stressor-induced shifts in predator–prey preferences and the possibility of trophic plasticity in response to temperature and upwelling. While we acknowledge that consumers likely adjust their feeding strategies under environmental pressures, the primary goal of this study was to explore potential losses or gains of trophic and non-trophic interactions as community composition shifts in response to these stressors.

To address trophic plasticity explicitly, future studies should complement biodiversity (biomass and abundance counts) and physiological sampling (e.g. mortality and growth rates) of the mesocosm community with a direct sampling of trophic interactions. This could involve traditional gut content analyses, isotope analyses (Ito et al. 2024), or, preferably, metabarcoding of prey DNA and eDNA, estimating the relative proportion of prey consumed as well as allowing for the identification of small and cryptic prey items (Novotny et al. 2023). Moreover, if such information were available, alternative linear inverse modelling approaches to the currently used bioenergetic fluxweb model, such as LIM (van Oevelen et al. 2010), could be considered for the reconstruction of energy fluxes among species in the food web (Bourdaud et al. 2024). The advantage of LIM is that it enables the direct inclusion of physiological parameters (mortality, faecal export, growth rates, etc.) and isotope signatures alongside respiration rates to constrain the unknown energy flows among species (Bourdaud et al. 2024).

Another constraint of our study is the limited number of experimental units available, which limits the number of treatment levels and replicates. The aim was to design an experimental set-up that addresses the urgency of multiple-driver approaches (Boyd et al. 2018), here warming and upwelling, in realistically large and complex communities (1500 l mesocosms, holding multiple species). Regression designs are commonly applied in experiments of this scale (Cottingham et al. 2005, Taucher et al. 2017, Melzner et al. 2020, Wahl et al. 2021), representing powerful approaches in that they allow for capturing the nature of the ecological responses, such as non-linearities and potential tipping points (Boyd et al. 2018, Kreyling et al. 2018, Riebesell et al. 2023). While replication is ideal, it is often logistically unfeasible in large-scale mesocosm studies, and regression-based designs remain a robust alternative when the goal is to detect directional trends (Marshall 2024).

5. CONCLUSIONS

Warming was the main driver of restructuring coastal Baltic Sea communities in our mesocosm study, reducing biomass across trophic levels and ecological network complexity through losses of trophic and non-trophic interactions. The declines in the foundation species *Fucus* and the top consumer *Asterias* were key drivers of these changes. Our results suggest that future coastal systems may increasingly shift from canopy-forming macroalgal habitats toward simpler, filamentous algae-dominated food webs as ocean warming continues. Although based on simplified assumptions, our study highlights the importance of integrating trophic and non-trophic interactions in food web research. While we recognise the conceptual nature of this study, it provides a valuable framework for exploring how warming and multiple stressors may restructure ecological networks. To make more refined predictions of marine food web responses to global change drivers, future work should combine mesocosm experiments with direct observations of species ecological interactions. We are hopeful that this study can inspire future experimental research with a more mechanistic focus on food web responses to environmental change.

Data archive. Data are available in Zenodo at 10.5281/zenodo.17802760.

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