MATERIALS AND METHODS

Study site and experimental design

The experiment was conducted in the Kiel Outdoor Benthocosm (KOB) system in the Kiel Fjord, Germany, a mesocosm infrastructure comprising twelve 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). For a detailed description of the KOB infrastructure, the experimental setup, and the specific environmental conditions of this experiment, see Wahl et al., (2015) and Wahl et al., (2021), respectively. The experiment ran for a total of 132 days (~4.5 months) between May 2nd and September 11th 2018. The mesocosms were supplied with through-flowing fjord water, and the entire water volume of each tank was replaced about seven times per day.

Six warming scenarios were implemented, ranging from naturally fluctuating (ambient) fjord temperatures to +5 °C above ambient (0–5 °C in 1 °C increments), representing a gradient of marine heatwave intensities. The warming treatments covered the range of temperature increases projected to occur in the Baltic Sea by 2050 to 2200 (under the RCP8.5 scenario; Meier et al., 2022). In 2018, natural Kiel Fjord temperatures were characterised by considerable temperature fluctuations and two recorded naturally occurring marine heatwaves encompassing an extremely warm summer (SI Fig. S1). Details on the average, maximum and range of temperatures observed are presented in SI Table S1.

The experimental set-up, which addresses the urgency of multiple drivers approaches (Boyd et al., 2018), here warming and upwelling, in realistically large and complex communities (1500 L mesocosms, holding multiple species), constitutes a non-replicated regression design (see below for information on the statistical analysis). Regression designs are commonly applied in experiments of this scale (Cottingham et al., 2005; Melzner et al., 2020; Taucher et al., 2017; Wahl et al., 2021) and are powerful in that they allow us to capture 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).

Temperature, salinity, pH, and oxygen levels were consistently monitored throughout the experiment (SI Fig. S2). In half of the twelve tanks, the added warming of 0–5 °C was interrupted by three simulated upwelling events (July 3rd – 9th, August 4th – 11th, and August 28th – September 3rd, 2018; SI Figs S1–S2) by switching to another water intake pipe at 14 meters depth (i.e., below the thermocline). Upwelled waters were cooler, poorer in oxygen, lower in pH, and more saline (SI Fig. S2), which is characteristic of upwelling events in the Kiel Fjord during the summer season (Wahl et al., 2021). Oxygen levels were low, and the water was hypoxic (<2 mg L^{-1}), mainly during the third simulated upwelling event (SI Fig. S2). For more in-depth information about the warming scenarios, temperature fluctuations over the study period, and simulated upwelling, see Wahl et al., (2021).

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* and *Fucus serratus* were added to the tanks, as well as their associated mesograzers at mean densities found in the macroalgae on the sampling date. Due to a later start in their growth season, fronds of the non-indigenous red alga *Gracilaria vermiculophylla* were distributed into the tanks 50 days 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 (Wahl et al., 2021). 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 not removed, as these also occur under natural conditions.

As substrate for the natural recruitment of soft-bottom fauna during the experiment, plastic containers 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) were hung from the side wall of each tank (see SI Table S2 for details on the experimental units). For further details on the stocking of the tank communities, see Wahl et al., 2021).

At the end of the experiment, the mesocosms were sampled for abundance and biomass data for all species within the tanks. Diverse sampling methods were employed for the different components of the experimental tanks (detailed in SI Table S2). Using certain methods, only abundance data were recorded (SI 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 (SI Methods, SI Table S3). 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 SI Table S2 and SI Methods). All species in the mesocosms were identified to the lowest possible taxonomic level (genus or species), except for microphytobenthos, phytoplankton, and detritus, which were aggregated into one node in the food web (i.e. Microalgae and Detritus).

Two predator species, the common sea star *Asterias rubens* and the green shore crab *Carcinus maenas*, were housed in separate compartments of the mesocosms but were not allowed to directly interact with or feed on the community that recruited in the mesocosms. Consequently, their role and impact considered in the food web analyses reflect potential, and not realised, interactions and energy flows.

Trophic network construction

Food webs are composed of nodes (S) and links (L) representing species and trophic interactions, respectively (Table 1, Fig. 1a). Trophic species can correspond to biological species, groups of organisms that share the same set of predators and prey, and non-living components of matter and energy, such as detritus (Dunne et al., 2002). Data on trophic interactions were collated through an extensive literature review of diet and feeding studies, expanding on previous work from the Baltic Sea (Kortsch et al., 2021; Olivier et al., 2024). Constructing food webs based on trophic interactions observed in the literature is common practice in food web studies (Delmas et al., 2019; Poisot et al., 2016). This approach represents ‘potential’ rather than ‘realised’ interactions among species. Here, we did not aim to document realised interactions but to illustrate the potential loss of both trophic and non-trophic interactions as species composition changes – whether through loss or gain – in response to environmental stressors. Following a thorough review process, some taxa still lacked sufficient diet information. In a few cases (8% of the final dataset), we inferred links by assuming that closely related species (species of the same genus or family) share predators and prey (Frelat et al., 2022; Olivier et al., 2019). The final data set underwent further verification in consultation with experts at GEOMAR Kiel, Germany. The constructed metaweb (Fig. 1) is available with references at Zenodo [DOI to be added].

Non-trophic network construction

In addition to feeding relationships, non-trophic interactions are important for structuring coastal communities. To investigate how non-trophic interactions change as a response to warming scenarios and upwelling, we mapped the following among the mesocosm species (Fig. 1): competitive (-/-), antagonistic (-/+), amensalistic (-/0), commensalistic (+/0), and mutualistic (+/+) interactions. Non-trophic interactions related to sediment burrowing activities (e.g., by clams) were not considered. Competitive interactions were derived from the food web by identifying species sharing prey items, and therefore potentially competing for the resource. Competitive interactions related to the node 'Microalgae and Detritus' were excluded, assuming that there is no limitation of these resources in the tanks. All other non-trophic interactions were based on a thorough literature review, local expert knowledge, and personal observations.

The metaweb for multiple interaction types consists of 188 links, out of which 114 are non-trophic interactions (Fig. 1). 60% of the non-trophic interactions are competitive, mostly involving mesograzers or top consumers. Most of the positive non-trophic interactions (commensalism and mutualism) arise through the structure or habitat provided by macrophytes to mesograzers, whereas herbivore partial grazing on basal species (non-lethal for the algae) constitutes the antagonistic interactions. Among herbivore species, the snails *Hydrobia* spp. and *Littorina* spp. were prominent, with a majority of their links being competitive non-trophic links (Fig. 1). Among the top consumers, the crab *C. maenas* and the polychaete *H. diversicolor* have the highest numbers of non-trophic links, mainly competitive interactions for prey items shared with other consumers. The non-trophic metaweb, along with references, can be accessed at Zenodo [DOI to be added]. To assess how non-trophic network structure varied across warming and upwelling scenarios, the network property number of non-trophic links was quantified.

Unweighted and weighted trophic network properties

To assess how food web structure and functions varied across the warming scenarios and the upwelling events, we quantified seven unweighted (topological) and two weighted (flux-based) network properties. 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 the mean level of omnivory (Omni; Table 1). In addition to these, we also assigned energy fluxes to the interactions using a bioenergetic food web modelling approach, which allows estimating food web functions such as changes in carnivorous fluxes and herbivorous fluxes. This bioenergetic modelling approach is based on allometric scaling relationships between metabolism, body mass, and temperature (Brown et al., 2004), and 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 detail on the bioenergetic model and model parameterisation, consult the supplementary information (SI Methods).

To test for the sensitivity of the fluxes and the herbivory and carnivory functions, we randomly sampled 1000 biomass estimates for each trophic species from a normal distribution with a mean equal to the originally estimated biomasses at the tank level and a standard deviation of 0.3. This resulted in 1000 different flux estimates per treatment, for which a median flux was calculated. Energy fluxes were calculated using the ‘fluxweb’ R package (Gauzens et al., 2019), and the food web metrics were calculated using custom-written code. The R package ‘igraph’ (Csárdi & Nepusz, 2006) was used to create the trophic as well as the non-trophic network graphs. The R code is available via Zenodo on GitHub [*DOI to be added*].

Statistical and numerical analyses

To analyse the relationships between biomass changes, food web metrics, and applied treatments (i.e., warming scenarios and upwelling events), we applied Generalized Additive Models (GAMs). 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 distribution assumptions. Each model includes smooth terms 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). Specifics about the fitted models, including their random effects, link functions, smooth terms, and error distributions are provided in the SI Methods and in SI Tables S4–S5. Further, to examine the most important associations among the food web metrics and functions, and warming and upwelling treatments, we applied a principal component analysis (PCA) using the R package ’factoextra’ (Kassambara & Mundt, 2020).

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