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Research

Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization

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Large-scale alterations in marine ecosystems as a response to environmental and anthropogenic pressures have been documented worldwide. Yet, these are primarily investigated by assessing abundance fluctuations of a few dominant species, which inadequately reflect ecosystem-wide changes. In addition, it is increasingly recognized that it is not species identity per se, but their traits that determine environmental responses, biological interactions and ecosystem functioning. In this study, we investigated long-term, spatio-temporal variability in trait composition across multiple organism groups to assess whether functional changes occur in a similar way across trophic levels and whether shifts in trait composition link to environmental change. We combined extensive trait datasets with long-term surveys (30–40 yr) of four organism groups (phytoplankton, zooplankton, benthic invertebrates and fish) in three environmentally distinct areas of a large marine ecosystem. We found similar temporal trajectories in the community weighted mean trait time-series of the different trophic groups, revealing ecosystem-wide functional changes. The traits involved and their dynamics differed between areas, concurrent with climate-driven changes in temperature and salinity, as well as more local dynamics in nutrients and oxygen. This finding highlights the importance of considering both global climate, as well as local external drivers when studying ecosystem changes. Using a multi-trophic trait-based approach, our study demonstrates the importance of integrating community functional dynamics across multiple trophic levels to capture ecosystem-wide responses which could, ultimately, help moving towards a holistic understanding, assessment and management of marine ecosystems.

Keywords: climate change, community dynamics, eutrophication, functional reorganisation, multi-trophic, temperature



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Introduction

Marine communities worldwide are undergoing large-scale changes in response to environmental and anthropogenic impacts, including fishing, eutrophication, pollution and habitat destruction (Millennium Ecosystem Assessment 2005). These alterations in community composition and species abundances can be linked to changes in species distributions (Pinsky et al. 2011, Hiddink et al. 2015), phenology (Edwards and Richardson 2004) and trophic mismatch (Durant et al. 2007), and have been documented across a range of marine organism groups from primary producers to top predators (Poloczanska et al. 2013). While our understanding of ecological community changes is advancing, the dynamics of biological systems are mostly studied by focusing on single organism groups. Yet, organisms across groups are connected through biotic interactions and shared environmental conditions (Fig. 1). The importance of interactions across trophic levels can be illustrated through documented regime shifts and trophic cascades (DeYoung et al. 2008), for instance the cascading effects of the loss of marine top predators on the abundances of the lower trophic levels (Baum and Worm 2009, Casini et al. 2012). Multi-trophic community reorganization has also been linked to environmental change, such as shifts in large-scale hydro-meteorological forcing (Anderson and Piatt 1999, Beaugrand 2004, Lindegren et al. 2018) or heatwaves (Ruthrof et al. 2018). It is therefore crucial to understand how environmental and anthropogenic pressures affect not only the commercially most important taxa (e.g. fish), but all organisms across trophic levels.

It is increasingly recognised that species traits (i.e. morphological, demographic or physiological attributes; Violle et al. 2007), rather than their taxonomic identity, determine their responses to the environment (Keddy 1992, Diaz et al. 1998). Hence, the use of traits provides a more mechanistic approach to understanding changes in community composition in comparison to more case-specific taxonomic information (McGill et al. 2006, Shipley et al. 2006). For example,

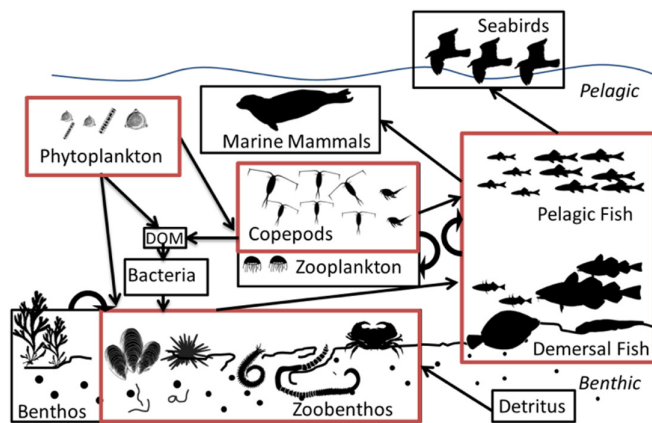


Figure 1. Schematic representation of the different organism groups in the Baltic Sea food web (HELCOM 2018). The groups analysed in this study are highlighted in red.

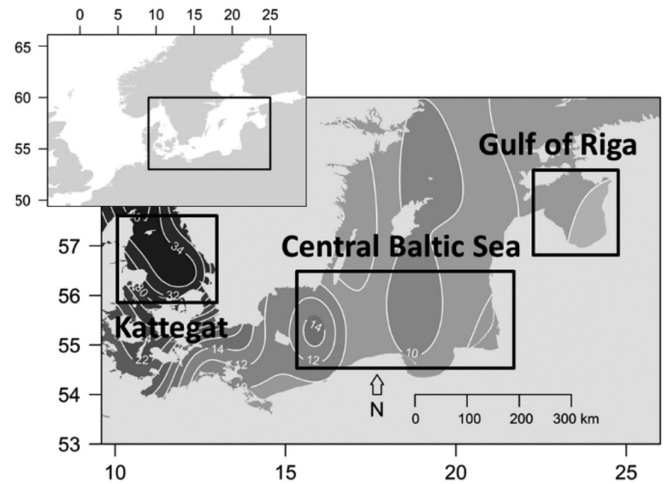


Figure 2. Map of the southern part of the Baltic Sea with the location of the three case study systems. The white contour lines represent areas with similar levels of bottom-water salinity (salinity levels shaded in grey).

community traits of benthic invertebrates are often scrutinized to investigate the impacts of bottom trawling, with species characterized by long lifespan or epifaunal position being less abundant in highly disturbed communities (De Juan et al. 2007, Rijnsdorp et al. 2018). Moreover, trait identity and diversity are linked to ecosystem functions (Diaz and Cabido 2001, Gagic et al. 2015) from which important ecosystem services can be derived, such as seafood and climate regulation. In benthic communities, traits such as the method of resource capture can influence the marine carbon cycle (Bremner 2008), whereas the mode of sediment mixing can impact nutrient fluxes (Norling et al. 2007). Thus, there is a need for characterising community composition not only in terms of species abundances, but also in terms of their trait composition across multiple trophic levels. By adopting such a multi-trophic trait-based approach we may foster more mechanistic understanding of marine ecosystem dynamics, and develop holistic ecosystem-based approaches to marine management (McLeod and Leslie 2009).

The main objective of this study is to evaluate and compare temporal variability in the trait composition of multi-trophic communities across three areas of a large marine ecosystem, the Baltic Sea, that are characterised by different environmental conditions and community composition (Fig. 2). The Baltic Sea has experienced pronounced ecological modifications with a major restructuring of the offshore food web in the late 1980s (Möllmann et al. 2009, Casini et al. 2012). These ecological changes have been associated with increasing temperature, reduced salinity and oxygen concentrations, as well as high anthropogenic pressures, including eutrophication and commercial fishing (Lindegren et al. 2009, Möllmann et al. 2009, Korpinen et al. 2012, Reusch et al. 2018). In recent years, a nutrient reduction scheme was implemented with spatially variable success (HELCOM 2018). In addition, the Baltic Sea has experienced a warming rate that exceeds the global ocean average, which might

offset the effects of nutrient reduction on the decrease of hypoxic areas and thus the rebuilding of the benthic communities (Reusch et al. 2018). Due to available long-term datasets combined with high environmental impact from ongoing climate change and recent nutrient management, the Baltic Sea is an ideal ecosystem to investigate dynamics of multi-trophic communities, and how they relate to environmental variability. Here, we integrate long-term community composition and trait information across four major organism groups composing the food web (i.e. phytoplankton, zooplankton, benthic invertebrates and fish, Fig. 1) to assess temporal changes in multi-trophic trait composition. We investigate whether there are any consistent temporal patterns in the community weighted mean traits across organism groups, whether these dynamics are consistent between areas, and whether the emerging trends can be explained by environmental and anthropogenic factors.

Material and methods

Community composition

The multi-trophic trait composition was assessed in three areas of the Baltic Sea, each characterised by different environmental conditions, dynamics and species richness: from the saline and relatively species-rich Kattegat, to the brackish and species-poor Central Baltic Sea and the shallow Gulf of Riga (for more information on the studied areas see Supplementary material Appendix 1). Community composition (i.e. the relative abundance of species in a given location) for the three areas were obtained from long-term scientific surveys and one fish stock assessment, spanning 30–40 yr from the early 1980s to early 2010s (Supplementary material Appendix 1 Table A1). Among the surveys, six used a fixed set of stations sampled throughout the studied period: the phytoplankton surveys in the three areas, zooplankton surveys in Kattegat and Central Baltic Sea, and the benthic invertebrates (hereafter benthos) survey in the Gulf of Riga. Conversely, five surveys used random or semi-randomized sampling schemes with a varying number of stations sampled every year: fish surveys in Kattegat and Gulf of Riga, benthos surveys in Kattegat and Central Baltic Sea and the zooplankton survey in the Gulf of Riga. Because estimates of community composition and diversity can be affected by sampling effort (Magurran and McGill 2011), we standardised the sampling effort (in terms of number of samples) for these five surveys. We used sample-based rarefaction for each time-series, fixing the number of samples per year from which the annual community composition was calculated. This fixed number of samples (n) varies between surveys and was determined as a trade-off between using a sufficiently high n and not eliminating too many years during which fewer than n samples were taken (resulting in n varying from three to 10 depending on the survey, Supplementary material Appendix 1 Table A1). The community composition was obtained by performing

1000 bootstraps of n samples for each year. For example, for benthos in Kattegat, n was set to four. Thus, for each year we assembled 1000 benthos communities, which were calculated as the sum of the species abundances in four randomly selected samples from this given year. Years with fewer than four samples were eliminated from the data (Supplementary material Appendix 1 Fig. A1). For the six surveys with stations that were geographically fixed and sampled every year, no standardization of sampling effort was needed as the same number of samples was used every year to derive community composition. For fish in the Central Baltic Sea, no long-term survey data was available. Instead, we used abundance estimates from a stock assessment model for the three main fish species: cod *Gadus morhua*, sprat *Sprattus sprattus* and herring *Clupea harengus*. These three fish species are highly dominant in the Central Baltic Sea, accounting for more than 95% of the total fish community abundance in the scientific survey data, and therefore largely characterise the fish community in terms of abundance in this area (Supplementary material Appendix 1 Fig. A2).

As our analysis focuses on offshore community composition, only survey stations deeper than 10 m were considered to avoid sampling of coastal communities. The benthos communities analysed here correspond to the macrofauna (> 1 mm), as smaller species (e.g. meiofauna) are not successfully retained in the sieve. The zooplankton communities include only copepods as this sub-class was thoroughly sampled and identified in comparison to the other zooplankton groups (e.g. cladocerans, rotifera). Copepods are the preferred prey of Baltic Sea zooplanktivorous fish (sprat and herring; Möllmann et al. 2004, Ojaveer et al. 2018), and they dominated the biomass composition of zooplankton communities from the studied areas. To ensure the robustness of the results, we performed additional analysis which included the abundance of the cladocerans, the second most abundant zooplankton group. Ciliates (microzooplankton) identified in the phytoplankton samples were eliminated, whereas identified cyanobacteria and mixotrophic or heterotrophic dinoflagellates were kept in the phytoplankton communities.

Trait information

For each organism groups we selected a set of key traits that broadly characterize the fundamental activities of a species, namely to feed, grow and reproduce (Supplementary material Appendix 1 Table A2). Although the trait categories differ between groups, the selected set of traits permits us to characterise and assess changes in the main life-history strategies of multi-trophic communities. The traits selected to characterize the changes in the fish community were: body size (maximum fork length), habitat position (demersal or pelagic), feeding group (benthivorous, piscivorous, planktivorous), offspring size and parental care. The trait values were obtained from Pecuchet et al. (2017). The selected benthos traits were: body size (average adult length), seabed position (epibenthic, interface, top, middle-deep), feeding

group (suspension feeder, deposit feeder, scavenger and predator) and developmental mode (fragmentation–fission, direct, lecithotrophic, planktotrophic). The benthos traits were obtained from Törnroos et al. (2015). The traits characterising zooplankton were: body size (average adult female length), free spawner, production of resting eggs, feeding behaviours (cruise feeder, ambush feeder and feeding-current feeder) and feeding group (herbivore, carnivore). The zooplankton traits were obtained from Brun et al. (2016). The selected phytoplankton traits were: cell volume, energy pathway (autotrophy and heterotrophy), motility, possibility of forming chain and presence of silica cell wall. The phytoplankton traits were obtained from Klais et al. (2016a). For the feeding-related traits of benthos, zooplankton and fish, the category scores were assessed as one divided by the number of realised feeding categories if a species was feeding on multiple categories. We did not take into account the number of prey species or their abundances in the diet, but just whether the feeding categories are expressed or not (i.e. equal weight). For example, for an omnivorous zooplankton species the scores would be 0.5 for herbivore and 0.5 for carnivore.

Not all surveys used the same taxonomic recording; therefore, species scientific names were checked against the World Register of Marine Species (<www.marinespecies.org>) and updated by the ‘accepted’ scientific name when appropriate. For some species, this resulted in taxonomic recording specified to a higher taxonomic level, e.g. genus or family. For these records, we assigned the average traits of all informed species belonging to the same genus or family in our trait tables. For each species, only one value per trait was used. Consequently, we do not consider potential intra-specific changes in trait values over time and thus assume that inter-species variability is higher than intra-species variability. However, we do acknowledge that intra-specific trait variability can be important in reshaping community composition and that it needs further investigations.

Environmental variables

To test whether the observed dynamics of the multi-trophic trait composition could be linked to environmental changes, we included variables that are known to impact the organisms in the area: temperature, salinity, nutrient concentration (i.e. nitrogen and phosphate) and oxygen (Diekmann and Möllmann 2010). The variable sources included both in situ observations and interpolated observations and due to data availability, the variable list differed slightly between the areas (see definitions, sources and units for all environmental variables in Supplementary material Appendix 1 Table A3). In addition, large-scale climatic indices (the Baltic Sea Index, BSI; the North Atlantic Oscillation Index, NAO; the Atlantic Multidecadal Oscillation AMO) were added to investigate potential impact of large-scale ocean-atmospheric forcing. To account for fishing impacts, commercial landings and catches of the main fish stock in the different areas were also included when available.

Multi-trophic trait-based analysis

Multiple factor analysis (MFA, Husson et al. 2018) was used to identify the main temporal dynamics of the multi-trophic community weighted mean (CWM) traits. For each organism group, CWM traits were calculated as trait values weighted by the log-transformed abundance of the species present in the community (Supplementary material Appendix 1 Fig. A3–A14). For the five surveys where 1000 random communities were assembled for each year, we used the median CWM trait values in the analysis. We used the median instead of the mean because it is more robust to outliers. Trait categories that are expressed on average by < 10% of the individuals in a community (time-series average of the median), or for which the median never exceeds 25% during any given year, were removed from the MFA as they were not considered key traits characterising the communities. All input variables were normalized to zero-mean and unit-variance to have the same weight in the analysis. We used all years for which at least three out of four organism groups had been sampled (Supplementary material Appendix 1 Fig. A1). Missing CWM values were imputed based on a regularized iterative multiple correspondence analysis (MCA) algorithm (Josse and Husson 2016) available in the missMDA R-package. Statistical analyses were done in R 3.6.1., and the MFA was performed with the package FactoMineR (Husson et al. 2018).

In comparison to the commonly used principal component analysis (PCA), the MFA takes into account the fact that the data is structured around groups (here different organisms) to balance the importance of each group in the analysis. This characteristic is especially important when the groups are described by a different number of traits. In addition, extra variables can be added in the MFA. These variables do not influence the result of the analysis, which is solely based on the CWM traits time-series, but their loadings can be visualized in relation to the main axes of CWM traits variability, giving an indication on how the temporal dynamics of these other variables relate linearly to the observed dynamics in the CWM traits. To test whether the observed dynamics of the multi-trophic trait composition could be related to changes in environmental variables and relative abundance of key taxa, we included these variables in the analyses. Although species typically show unimodal responses to the environment, we assume that over the limited range of environmental conditions within each case study area, the responses may be approximated by linear relationships.

Finally, we summarised the MFA results of the three areas by displaying and assessing temporal changes in variables that have high loadings (i.e. high correlations) on the first principal dimension (Dim 1), including both abiotic and anthropogenic variables. To visualise the main temporal development of the variables their linear or non-linear trends were assessed by using a linear model and a generalized additive model (GAM). For the GAM we used a smoothing spline function constrained to four degrees of freedom (mgcv package, Wood 2011). If both the linear and non-linear models were

significant, the model which explained the most deviance was reported in the summary figure.

Results

Kattegat

In Kattegat, the first dimension (Dim 1) accounts for 29% of the variability in multi-trophic CWM traits over time (Fig. 3a). Benthos, fish and zooplankton traits contribute to the variability explained by Dim 1 with 43, 27 and 26% respectively, whereas phytoplankton contributes with only 4% (Fig. 3a). Dim 1 displays a decreasing trend with low inter-annual variability and represents a relatively gradual change in the trait composition of the different community groups (Fig. 3a). The communities in the early 1980s are characterised by a relatively higher proportion of benthos with planktotrophic larvae and suspension-filter feeder traits; zooplankton species

that are cruise- or feeding-current feeders and free spawners, and fish species that are piscivorous and produce large offspring (Fig. 3c). Over time, the communities become more dominated by benthivorous fish, lecithotrophic larvae and deposit-feeder benthos, and ambush-feeding zooplankton (in the 2010s, Fig. 3c). The second dimension (Dim 2) explains 20% of the trait variability with phytoplankton contributing the majority (56%), whereas fish, zooplankton and benthos contributed only to 22, 19 and 4%, respectively (Fig. 3b). Dim 2 mainly captures the shift in the relative proportion of motile heterotroph phytoplankton to autotroph and chain-forming ones (Fig. 3e). This shift corresponds to a change in the ratio between diatoms and dinoflagellates in the community (Supplementary material Appendix 1 Fig. A15), with an increase of motile heterotroph species in the 1980s and a decrease in the 2000s.

Bottom-water temperature is the environmental variable with the highest loading along Dim 1 (0.82, Fig. 3d), followed by surface temperature, the AMO and bottom nitrate.

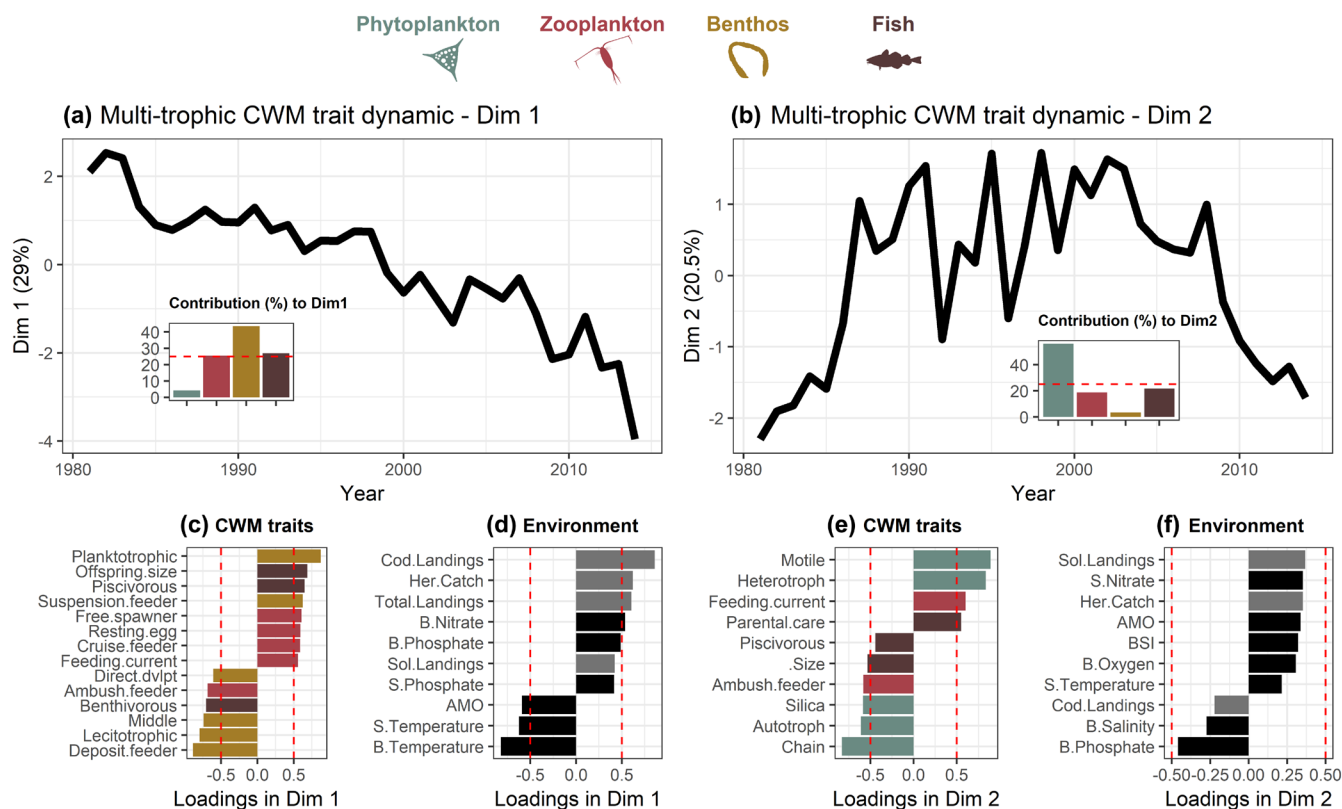


Figure 3. Temporal changes in the community weighted mean (CWM) traits of multi-trophic communities in the Kattegat obtained from a multiple factor analysis (MFA). Time-series of (a) the first dimension (Dim 1) and (b) of the second dimension (Dim 2) of multi-trophic CWM traits variability and the contribution of each trophic group to the observed dynamics. The red dotted line represents a contribution of 25%, the percentage that would be obtained if all the groups contributed equally to the dynamics. Loadings of the CWM traits along (c) Dim 1 and (e) Dim 2. Loadings of the environmental (black) and fishing-related (grey) variables along (d) Dim 1 and (f) Dim 2. High environmental loadings demonstrate co-variability between the environmental variables and the multi-trophic trait dynamics (Dim 1 and Dim 2). For clarity, we only represented the loadings that were higher than 0.5 (red dotted lines) or at minimum the ten highest ones. The loadings for the entire trait and environment variables are reported in Supplementary material Appendix 1. 'B.' refers to bottom, 'S.' refers to surface, 'Her' to herring *Clupea harengus*, 'Sol' to sole *Solea solea*, 'AMO' to the Atlantic Multidecadal Oscillation and 'BSI' to the Baltic Sea Index.

The fishing-related variables cod landings, total landings and herring catches also have a relatively high loading (> 0.5). On Dim 2, none of the variables have a loading greater than 0.5 suggesting that phytoplankton might respond non-linearly to the variables or be affected by other variables not tested here.

Central Baltic Sea

In the Central Baltic Sea, the Dim 1 accounts for 44% of the temporal variability in CWM traits across trophic levels (Fig. 4a). Zooplankton and fish traits contribute the most to Dim 1 with 33% each, followed by phytoplankton (26%), while benthos contributes to only 7%. The first dimension is characterised by a decrease from 1980s until the mid-90s and thereafter a stagnation or minor increase (Fig. 4a). In the early 1980s the communities are characterised by a larger proportion of feeding-current zooplankton, large piscivorous fish and large heterotroph phytoplankton, while from the late 1980s and onwards, the communities are characterised by a higher proportion of ambush-feeders and resting-egg producing zooplankton, planktivorous fish and autotrophic phytoplankton (Fig. 4c). Dim 1 notably reflects an increase in the abundance of the pelagic fish species sprat, and a decrease of cod (high loading along Dim 1, Supplementary material Appendix 1 Fig. A15). Dim 2 also explains a rather large part of CWM trait variability (27%) with benthos being the main contributor (46%), followed by zooplankton (25%),

phytoplankton (23%) and fish (7%, Fig. 4b). Dim 2 is characterised by high inter-annual variability and reflects fluctuations between benthos communities composed of epibenthic predator species and communities composed of large deposit-feeder species. The latter communities occur more frequently in recent years (Fig. 4e).

Surface salinity is the environmental variable with the highest loading along Dim 1 (0.81), followed by surface temperature (0.63). The fishing-related variables cod, herring and sprat catches also have loadings > 0.5 along the first axis. Bottom oxygen and total landings are the only variables with a loading > 0.5 along Dim 2.

Gulf of Riga

In the Gulf of Riga, Dim 1 accounts for 38% of the multi-trophic CWM trait dynamic with all groups contributing almost equally: phytoplankton (28%), zooplankton (25%), benthos (24%) and fish (23%, Fig. 5a). Dim 1 displays a decreasing trend with a high rate of change in the late 1980s to early 1990s (Fig. 5a). Communities in the early 1980s are characterised by large and silica-wall phytoplankton, deposit-feeder benthos, feeding-current feeders and herbivore zooplankton, and large and piscivorous fish (Fig. 5c). In comparison, communities in the early 2010s are characterised by motile heterotrophic phytoplankton; large and scavenging benthos; ambush-feeding zooplankton; and

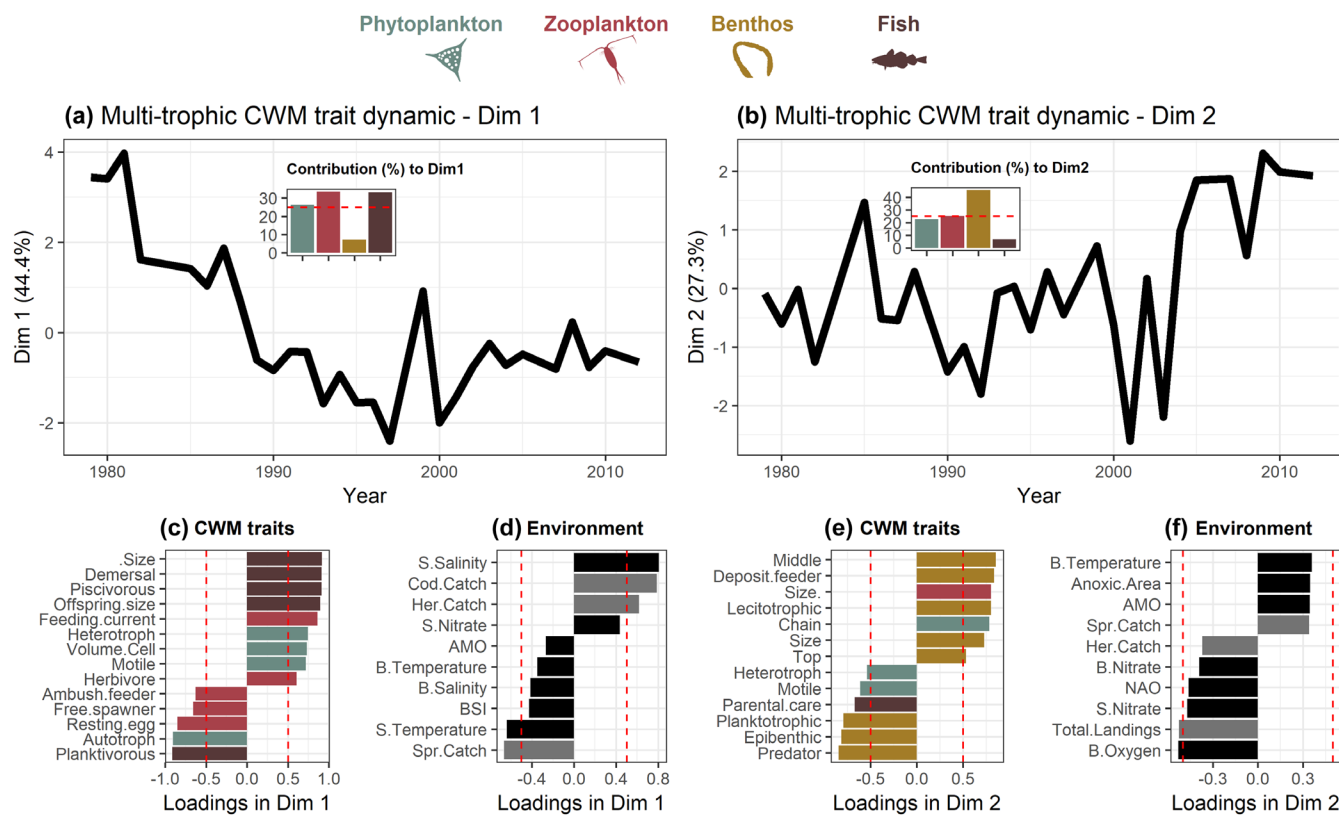


Figure 4. Temporal changes in the CWM traits of multi-trophic communities in the central Baltic Sea obtained from a multiple factor analysis (MFA). For detailed legend description see Fig. 3. ‘Spr’ refers to sprat *Sprattus sprattus*, ‘NAO’ to the North Atlantic Oscillation.

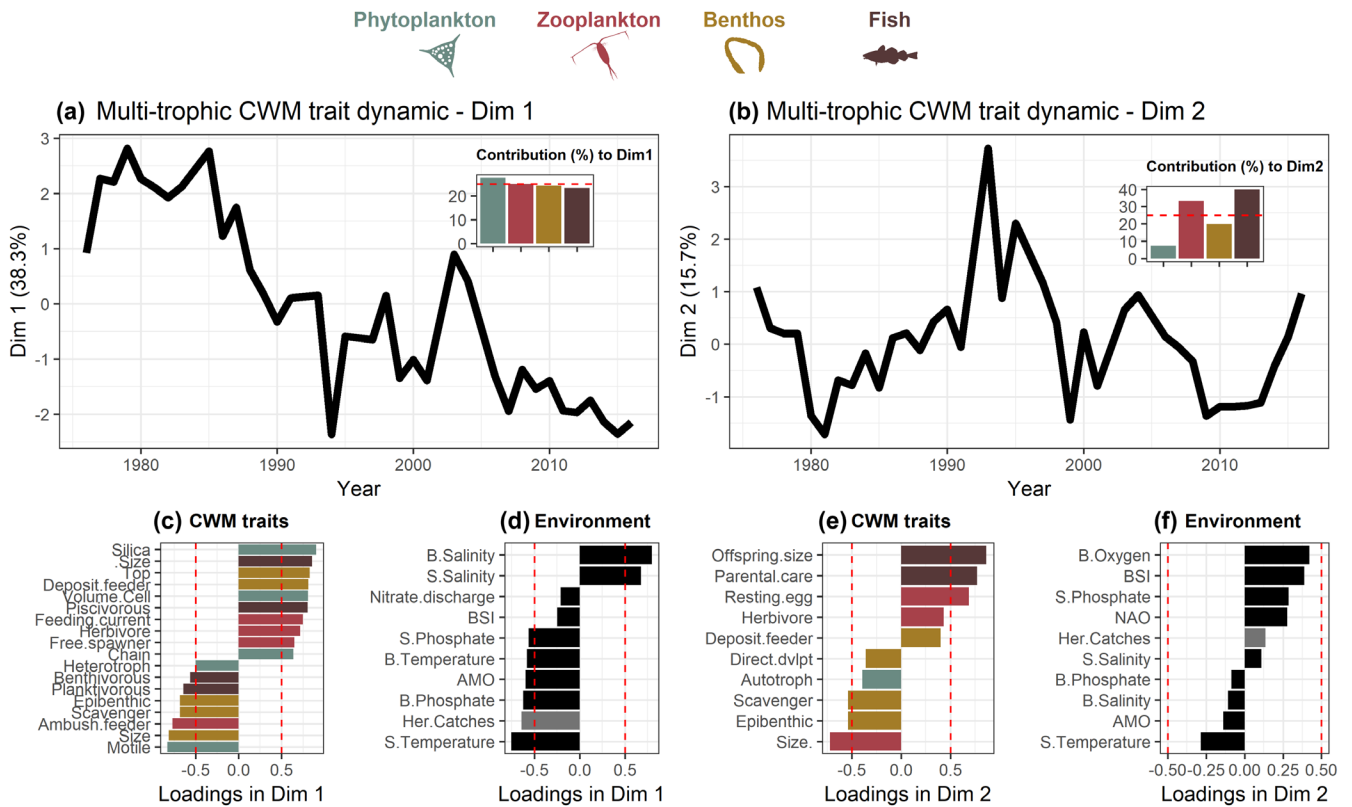


Figure 5. Temporal changes in the CWM traits of multi-trophic communities in the Gulf of Riga obtained from a multiple factor analysis (MFA). For detailed legend description see Fig. 3.

planktivorous- and benthivorous fish. Dim 1 reflects notably a decrease in the abundance of cod and diatoms during the studied period (high loading along Dim 1, Supplementary material Appendix 1 Fig. A15). The second dimension explains 16% of the trait variability with fish contributing the most (40%), followed by zooplankton (33%, Fig. 5b). Dim 2 does not follow any trend, but instead shows large fluctuations in the relative abundance of fish with high parental care and large offspring size and small resting-egg producer zooplankton (Fig. 5e).

Bottom salinity is the environmental variable with the highest loading along Dim 1 (0.80), followed by surface temperature (0.75, Fig. 5d). In addition, the AMO and phosphate, also have a loading greater than 0.5 (Fig. 5d). The fishing-related variable, herring catches, has a relatively high loading. None of the variables have a loading above 0.5 along Dim 2.

Summary of the observed ecosystem changes

In all three studied regions, we observe long-term functional reorganisations of the multi-trophic communities (Fig. 6). The inclusion or exclusion of the cladocerans in the zooplankton communities does not impact the main dynamic (Dim 1, Supplementary material Appendix 1 Fig. A16). There are commonalities between the temporal development of the multi-trophic trait composition and the environmental and

anthropogenic variables. Changes in the trait composition of the Kattegat multi-trophic communities are concomitant with a decrease in bottom nitrate and increase in temperature, as well as a decrease in cod and total fisheries landings (Fig. 6). Changes in the trait composition of the Central Baltic Sea and Gulf of Riga multi-trophic communities are both concomitant with a decrease in salinity, with a similar rapid change in the late 1990s and thereafter a stagnation or minor increase, and an increase in temperature. In addition, the multi-trophic trait dynamics are paralleled by changes in the landings and catches of the principal fish stock in the two areas (Fig. 6).

Discussion

We observed long-term functional reorganization across the three distinct areas in the Baltic Sea (Fig. 6). These reorganizations were driven by trait variability across multiple organism groups, reflecting ecosystem-wide changes throughout the region (Diekmann and Möllmann 2010). Previous work on multi-trophic communities found divergent directional trends across taxa when looking at aggregated trait diversity metrics, such as turnover, divergence or evenness (Concepción et al. 2017, Magurran et al. 2018, Törnroos et al. 2019). However, we show that similar temporal trends can be found across multiple trophic levels

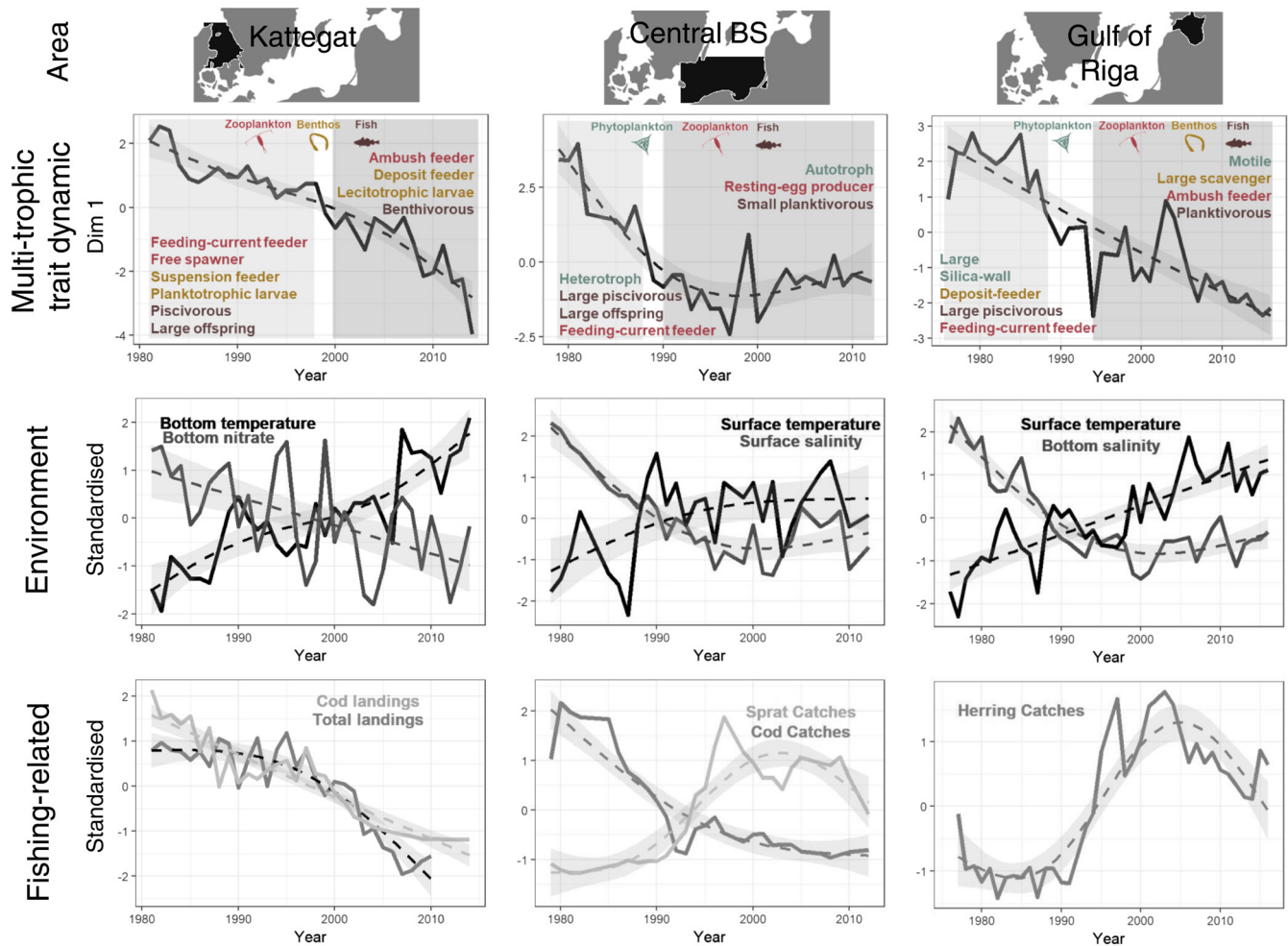


Figure 6. Summary of the main temporal variability in the three areas of the multi-trophic community weighted mean (CWM) dynamic (Dim 1, upper panel), environmental conditions (middle panel) and fishing pressures (lower panel). The CWM traits reported in the upper panel were selected due to their high loading along Dim 1. They represent a change in the trait composition of the multi-trophic communities from traits being relatively important in the early time-period (light grey area, positive loadings) to a decrease importance of these traits and increase importance of other traits in the later time-period (darker grey area, negative loading on average). The environmental and fishing variables were selected because they had a similar temporal pattern than the multi-trophic CWM dynamic (high loading along Dim 1). Dotted lines represent significant ($p < 0.05$) temporal linear or non-linear trends (GAM) with their confidence intervals shaded in grey.

when performing an integrated analysis of community traits across groups. The observed ecosystem-wide restructuring consisted of communities with different trait composition in the early 1980s compared to the 2010s. The traits that drove the changes varied between areas, but commonalities were also found. For instance, there was a general decrease in the relative abundance of piscivorous fish and an increase of ambush feeder copepods at the expense of feeding-current zooplankton (Fig. 6). The multi-trophic communities appear to respond to climatically driven changes in temperature and salinity, but also to local processes such as eutrophication (e.g. oxygen and nutrient concentrations) and fishing pressures (Fig. 6).

Baltic Sea temperatures have been rapidly increasing, with a warming exceeding the global average (Reusch et al. 2018). At a regional scale, several studies have showed that species

following a similar abundance trajectory in response to warming, also tend to share similar traits, e.g. small size, early-maturation and short lifespan (ter Hofstede and Rijnsdorp 2011, Pecuchet et al. 2017, Beukhof et al. 2019). Here, we did not find a consistent relationship between temperature and traits across areas and organisms. Instead, warming might be promoting trait turnover in the communities by acting on the relative abundances of the species already present in the local species pool (Hillebrand et al. 2010). In this study, the multi-trophic communities appear to track local changes in temperature more closely than large-scale climate variability (i.e. NAO, AMO or BSI), while the importance of the later on functional reorganisations have been documented in neighbouring areas (McLean et al. 2018).

Salinity was the environmental variable most strongly correlated to the observed multi-trophic CWM trait changes in

the Central Baltic Sea and the Gulf of Riga. In the same way as temperature, the decrease in salinity in these two areas appear to promote trait turnover rather than to select for specific traits. Salinity is known to affect the abundance and distribution of many marine species, which are living at their physiological limits in these two areas, hence shaping community structural and functional composition (Ojaveer et al. 2010, Törnroos et al. 2015, Pecuchet et al. 2016). Salinity affects a large spectrum of marine organisms ranging from plankton to fish (Lindegren et al. 2009, Olli et al. 2011, Eero et al. 2012, Otto et al. 2014), and consequently its decrease or increase has led to ecosystem-wide reorganizations (Möllmann et al. 2009, Diekmann and Möllmann 2010, Casini et al. 2012). Salinity decreased during the studied period due to less frequent inflow events from the neighbouring North Sea and an increase in freshwater run-off (Meier and Kauker 2003). The decrease in salinity was non-linear with a marked change in the late 1980s, reflected in the main temporal trajectory of the multi-trophic CWM traits (Fig. 6). A regime shift in the structural composition of the Baltic Sea food web in response to multiple pressures, including salinity, has been documented for the late 1980s (Möllmann et al. 2009, Diekmann and Möllmann 2010, Casini et al. 2012). Here, we show that the ecosystem changes were not only reflected in the structural- but also the functional composition of the multi-trophic communities.

Eutrophication is caused by high nutrient concentrations leading to enhanced primary production, which in turn can lead to oxygen depletion in bottom water (Conley et al. 2011, Carstensen et al. 2014). In Kattegat, the eutrophication status has been improving since the mid-1990s, whereas it has remained critical in most of the other Baltic Sea areas where the extent of anoxic waters is still widespread (Carstensen et al. 2014, HELCOM 2018). In our study, a gradual increase in the dominance of benthic species and their associated traits in Kattegat followed the decline in nutrient concentrations, hence supporting a potential shift from pelagic to benthic pathways and a recovery of the benthic compartment (Lindegren et al. 2012). In contrast, the seabed in the permanently anoxic basins of the central Baltic Sea is often referred to as a 'dead zone' due to the mass mortality and disappearance of benthos (Diaz and Rosenberg 2008, Gogina et al. 2016). In our analysis, benthos and fish communities in this area seem to follow different dynamics, with fish community variability contributing to the first axis of variation, whereas the benthos community contributes to the second axis, pointing towards a potential decoupling between the groups, as has been shown in coastal areas (Törnroos et al. 2019). The biological interactions between benthos and pelagic consumers are indeed expected to decrease under hypoxia or anoxia, impacting benthic–pelagic coupling (Griffiths et al. 2017).

Fishing selects for specific, mostly large-sized species, and as a result, modifies fish community composition, such as their size structure (Blanchard et al. 2005). Furthermore, the removal of large predatory fish can have cascading effects on lower trophic levels in marine ecosystems (Baum and Worm

2009, Casini et al. 2012). In addition, bottom trawling is known to impact benthic communities and to select for traits resistant to trawling (Sköld et al. 2018). In our analysis, fishing-related variables were correlated with the multi-trophic trait dynamics, particularly the decrease in large piscivorous fish in the three areas and benthic traits in the Kattegat. However, since causal relationships were not explicitly assessed in this study, we cannot assert that the observed multi-trophic dynamics are the outcome of fisheries impact on the community composition. Previous species-based studies in the Baltic Sea have, however, documented effects of fishing on fish community composition and food-web dynamics. This was notably observed in the responses of large piscivorous (e.g. cod) and benthivorous (e.g. flatfish) species to increases or decreases in fishing effort (Lindegren et al. 2009, Möllmann et al. 2009, Sköld et al. 2018).

Trait dynamics of multi-trophic communities are likely affected by both direct responses to these multiple environmental and anthropogenic pressures and indirect responses mediated by trophic interactions. For instance, the trait dynamics observed in the Central Baltic Sea and Gulf of Riga are thus likely resulting from the interactions of declining salinity, increasing temperature, fisheries, as well as the disappearance of cod, which is a top predator in these systems. In the 1980s, cod abundance was high in the Central Baltic Sea and as a result cod spread into the Gulf of Riga, while it later withdrew when its abundance declined due to unfavourable environmental conditions and high fishing pressure. The presence, and later disappearance, of this top predator induced a trophic cascade in the Gulf of Riga (Casini et al. 2012). Here, due to strong causal links between salinity, fisheries and cod abundance and no direct analyses of trophic interactions, the respective impacts of these variables on the multi-trophic trait dynamic cannot be assessed explicitly. Understanding the effect of trophic interactions on community composition is highly complex and requires information on feeding interactions, which were not available for this study. Integrating prey–predator interactions in trait-based approaches would be an important step forward and could bring novel insights into multi-trophic changes (Morales-Castilla et al. 2015, Nordström et al. 2015, Laigle et al. 2018).

In this study, we investigated ecosystem-wide temporal changes by studying community trait dynamics across multiple organism and areas. To encompass such a large taxonomic and spatio-temporal scale, the multi-trophic community composition was assembled from multiple data sources. This can influence the observed results due to differences in sampling methods and survey design. For instance, the phytoplankton and zooplankton data in the Kattegat and Central Baltic Sea were obtained from only one monitoring station that, although being representative of local changes, might not be enough to represent the entire studied area, as planktonic communities can show high spatial variability (Klais et al. 2016b). Further multi-trophic studies could be improved by using long-term monitoring data spanning multiple trophic levels, such as ecosystem-based monitoring

programs. In a time of global change, these integrated surveys are increasingly important to acquire knowledge on the interplay between the different food web compartments, predator–prey interactions and their link to environmental change (Kortsch et al. 2019).

Key functional traits influence, separately or in combination, a number of different ecosystem functions. One of the key novelties of a trait-based approach compared to a taxonomic approach lies in the switch towards an ecosystem-functioning perspective (de Bello et al. 2010, Maureaud et al. 2019), which ultimately could help understand the consequences for ecosystem services. The observed trait-based reorganizations could have implications for the functioning of the Baltic Sea ecosystem, including aspects of nutrient cycling, biomass production or benthic–pelagic coupling (Griffiths et al. 2017). For example, the observed decreasing abundance of demersal piscivorous fish (e.g. cod), and the resulting increase of small planktivorous fish could impact the benthic–pelagic energy transfer through increased modularity of the food web compartments (Kortsch et al. 2015), whereas the observed smaller size of phytoplankton cells could impact fish biomass production (Carozza et al. 2019). In addition, the observed reorganisations in functional composition across multiple trophic groups may likely have exacerbated impacts on ecosystems through cascading effects on ecosystem functions across trophic levels (Duffy et al. 2007, Soliveres et al. 2016) or altered resilience (Peterson et al. 1998).

Further ecosystem-level alterations in the Baltic Sea are expected in the future since temperature and salinity, identified as key drivers of the functional community change, are expected to increase and decrease, respectively, under ongoing climate change (Meier et al. 2012). Fresher and warmer waters will further reduce the abundance and distribution of marine species whereas the habitat of freshwater species may expand (Mackenzie et al. 2007), likely promoting trait turnover in the communities. Meanwhile, ongoing management and successful implementation of nutrient reduction in the Baltic Sea might help to rebuild a healthier benthic ecosystem, although benthic recovery might be hindered by warming. These changes will ultimately affect ecosystem functioning and services, such as fisheries. In order to prepare for and adapt to climate change, we argue that a multi-trophic functional approach like the one implemented here could help moving towards a holistic understanding, assessment and management of marine ecosystems in the Baltic Sea and beyond.

Data availability statement

The trait information is available in: doi.org/10.1016/j.seares.2014.04.010 (benthos), doi.org/10.1594/PANGAEA.868610 and doi.org/10.3354/meps11613 (fish), doi.org/10.1594/PANGAEA.862968 (copepod), <www.riinaklais.com/phytotraits> (phytoplankton). Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.d2547d7zb>> (Pecuchet 2019).

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Author contributions – LP, ML, SAO and MN conceived the ideas and designed methodology. All authors collected the data; LP analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supplementary material (available online as Appendix ecog-04643 at <www.ecography.org/appendix/ecog-04643>). Appendix 1.