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Disentangling temporal food web dynamics facilitates understanding of ecosystem functioning

Susanne Kortsch[1] | Romain Frelat[2] | Laurene Pecuchet[1,3] | Pierre Olivier[1] | Ivars Putnis[4] | Erik Bonsdorff[1] | Henn Ojaveer[5,6] | Iveta Jurgensone[7] | Solvita Strāķe[7] | Gunta Rubene[4] | Ēriks Krūze[4] | Marie C. Nordström[1]

[1]Environmental and Marine Biology, Åbo Akademi University, Turku, Finland; [2]Wageningen University & Research, Wageningen, The Netherlands; [3]UiT - The Arctic University of Norway, The Norwegian College of Fishery Science, Tromsø, Norway; [4]Institute of Food Safety, Animal Health and Environment BIOR, Riga, Latvia; [5]Pärnu College, University of Tartu, Pärnu, Estonia; [6]National Institute of Aquatic Resources, Technical University of Denmark, Lyngby, Denmark and [7]Latvian Institute of Aquatic Ecology, Riga, Latvia

Correspondence
Susanne Kortsch
Email: susanne.kortsch@gmail.com

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Abstract

1. Studying how food web structure and function vary through time represents an opportunity to better comprehend and anticipate ecosystem changes. Yet, temporal studies of highly resolved food web structure are scarce. With few exceptions, most temporal food web studies are either too simplified, preventing a detailed assessment of structural properties or binary, missing the temporal dynamics of energy fluxes among species.

2. Using long-term, multi-trophic biomass data coupled with highly resolved information on species feeding relationships, we analysed food web dynamics in the Gulf of Riga (Baltic Sea) over more than three decades (1981–2014). We combined unweighted (topology-based) and weighted (biomass- and flux-based) food web approaches, first, to unravel how distinct descriptors can highlight differences (or similarities) in food web dynamics through time, and second, to compare temporal dynamics of food web structure and function.

3. We find that food web descriptors vary substantially and distinctively through time, likely reflecting different underlying ecosystem processes. While node- and link-weighted metrics reflect changes related to alterations in species dominance and fluxes, unweighted metrics are more sensitive to changes in species and link richness. Comparing unweighted, topology-based metrics and flux-based functions further indicates that temporal changes in functions cannot be predicted using unweighted food web structure. Rather, information on species population dynamics and weighted, flux-based networks should be included to better comprehend temporal food web dynamics.

Susanne Kortsch and Romain Frelat shared first authorship.

4. By integrating unweighted, node- and link-weighted metrics, we here demonstrate how different approaches can be used to compare food web structure and function, and identify complementary patterns of change in temporal food web dynamics, which enables a more complete understanding of the ecological processes at play in ecosystems undergoing change.

1 | INTRODUCTION

Ecological community structure varies over different temporal scales (days, seasons, years, centuries), encompassing fluctuations in both abiotic drivers (temperature) and biotic processes (phenological responses, migrations, population dynamics). Temporal turnover in species composition and biomass structure can affect food webs via losses and gains of trophic interactions (i.e. links), or by influencing the magnitude of existing interactions without necessarily triggering their complete removal or addition (Bartley et al., 2019; Pecuchet, Blanchet, et al., 2020). There is a growing interest in understanding the underlying processes and mechanisms that govern temporal variability of ecological networks in order to better understand and anticipate how ecological networks vary through time and respond to future environmental scenarios (CaraDonna et al., 2020; Griffith et al., 2019; McMeans et al., 2015; Poisot et al., 2015; Trøjelsgaard & Olesen, 2016; Ushio et al., 2018; Yletyinen et al., 2016). However, temporal biotic processes at lower organisational levels related to changes in species composition and biomass are rarely, or with few exceptions (Baird & Ulanowicz, 1989; Boit & Gaedke, 2014), linked to higher system-level processes such as long-term variability in energy flux distributions.

Most temporal food web studies are limited to binary descriptions (based on presence/absence of species), relatively small networks (such as the Skipwith pond food web, Warren, 1989; the Elm flux or the Arctic tundra food webs, Schoenly & Cohen, 1991) or consider only few time steps, such as before and after scenarios (Jonsson et al., 2005; Kaartinen & Roslin, 2012; Kortsch et al., 2015; Pecuchet, Blanchet, et al., 2020; Yletyinen et al., 2016). Therefore, our current empirical understanding of how highly resolved food webs vary through time comes predominantly from a binary (i.e. presence/absence-based) perspective, ignoring potential asymmetries in the magnitude of trophic interactions. Unlike binary descriptions, weighted networks offer the opportunity to account for more subtle fluctuations in community structure through changes in species' biomasses or fluxes rather than through loss or gains of species (Bersier et al., 2002; Olivier et al., 2019). The magnitude of feeding interactions, or link weights, can be estimated in a number of ways (Berlow et al., 2004). In this study, we define link weights as the amount of energy flux among species. Energy fluxes are derived from species-level parameters related to the metabolic theory of ecology and biomass information using a bioenergetic model (Barnes et al., 2018; Gauzens et al., 2019), and can be regarded as proxies for

ecosystem functioning by describing the way energy flows among species (Barnes et al., 2018; Gauzens et al., 2019). This information provides an opportunity to compare temporal food web structure and function (Thompson et al., 2012). Here, functions of interest are total fluxes to specific functional feeding guilds (e.g. zooplanktivory is calculated as the total fluxes from zooplankton to their consumers).

It remains unclear how ecological network structure varies through time. Evidence from unweighted food webs suggests that food web macro-descriptors appear largely invariant at a wide range of temporal scales (Dunne et al., 2008; Griffith et al., 2019; Trøjelsgaard & Olesen, 2016; Yletyinen et al., 2016), although a recent study on binary plant–animal networks exhibited substantial temporal variability, in particular at finer temporal scales (i.e. diurnal and seasonal networks; CaraDonna et al., 2020). In contrast, link-weighted food webs have exhibited considerable variability in network structure over time in response to succession (Boit & Gaedke, 2014), or in response to perturbations such as invasion or removal of key species (Paine, 1980; Zaret & Paine, 1973). These divergent conclusions on food web responses to species fluctuations are likely the result of analyses based on different network types (unweighted vs. weighted), different network resolutions (Rasmussen et al., 2013), and different temporal scales (CaraDonna et al., 2020). Yet, looking beyond these opposing views, the classic empirical example of keystone predation clearly illustrates that species dynamics (i.e. combinations of strong and weak interactions) and food web structure (particular topological configurations) are interdependent, that is, dynamics constrain structure and vice versa (Berlow et al., 2004; Paine, 1966, 1980), which has also been confirmed by theory (Wootton & Stouffer, 2016). This interdependency between food web topology and species population dynamics calls for a combination of unweighted (topology-based) and weighted (e.g. flux-based) food web network approaches as key for understanding how ecological communities function.

Despite the growing interest in analysing temporal variability of food webs as well as linking structural and functional food web changes (Poisot et al., 2015; Thompson et al., 2012), to our knowledge, there have been no studies exploring the relationship between long-term food web structure and function combining unweighted and weighted food web approaches. Yet, a diverse set of approaches may highlight different patterns of change in temporal food web dynamics related to different ecosystem processes (Banašek-Richter et al., 2009; Bersier et al., 2002; Boit & Gaedke, 2014; Olivier et al., 2019). Here, we combined an unweighted (i.e. binary- and topology-based), a node-weighted

(biomass-based) and a link-weighted (flux-based) approach to study multi-decadal (1981–2014) food web dynamics in the Gulf of Riga, a brackish-marine sub-basin of the Baltic Sea with at least one major documented ecosystem shift during our study period (Arula et al., 2014; Casini et al., 2012; Einberg et al., 2019). At the end of the 1980s, the Gulf of Riga underwent an ecosystem-wide structural and functional reorganisation (Pecuchet, Lindegren, et al., 2020), which has been related to the disappearance of cod, a top predator in the ecosystem, and increases in the pelagic compartment associated with abrupt changes in environmental conditions (Casini et al., 2012; Pecuchet, Lindegren, et al., 2020). Being a well-studied aquatic ecosystem affected by multiple stressors, the Gulf of Riga provides an ideal case study to explore long-term trends and variability in food web structure and function. To study these temporal trends and variability, we asked the following questions: (a) how does food web structure and function vary over

a 34-year study period (1981–2014); (b) do unweighted and weighted food web approaches highlight different (or similar) aspects of temporal food web dynamics?; and (c) are the Gulf of Riga food web time series characterised by periods with distinct structure and function?

2 | MATERIALS AND METHODS

2.1 | Description of the study area

The Gulf of Riga is a relatively shallow (27 m mean depth) brackish sub-basin of the Baltic Sea connected to the central Baltic Proper (Figure 1a). Most of its freshwater comes from a large drainage area in the southern part of the basin (Kotta et al., 2008). In the offshore areas of the Gulf, average salinity is about 5.0–6.5 psu with the absence of
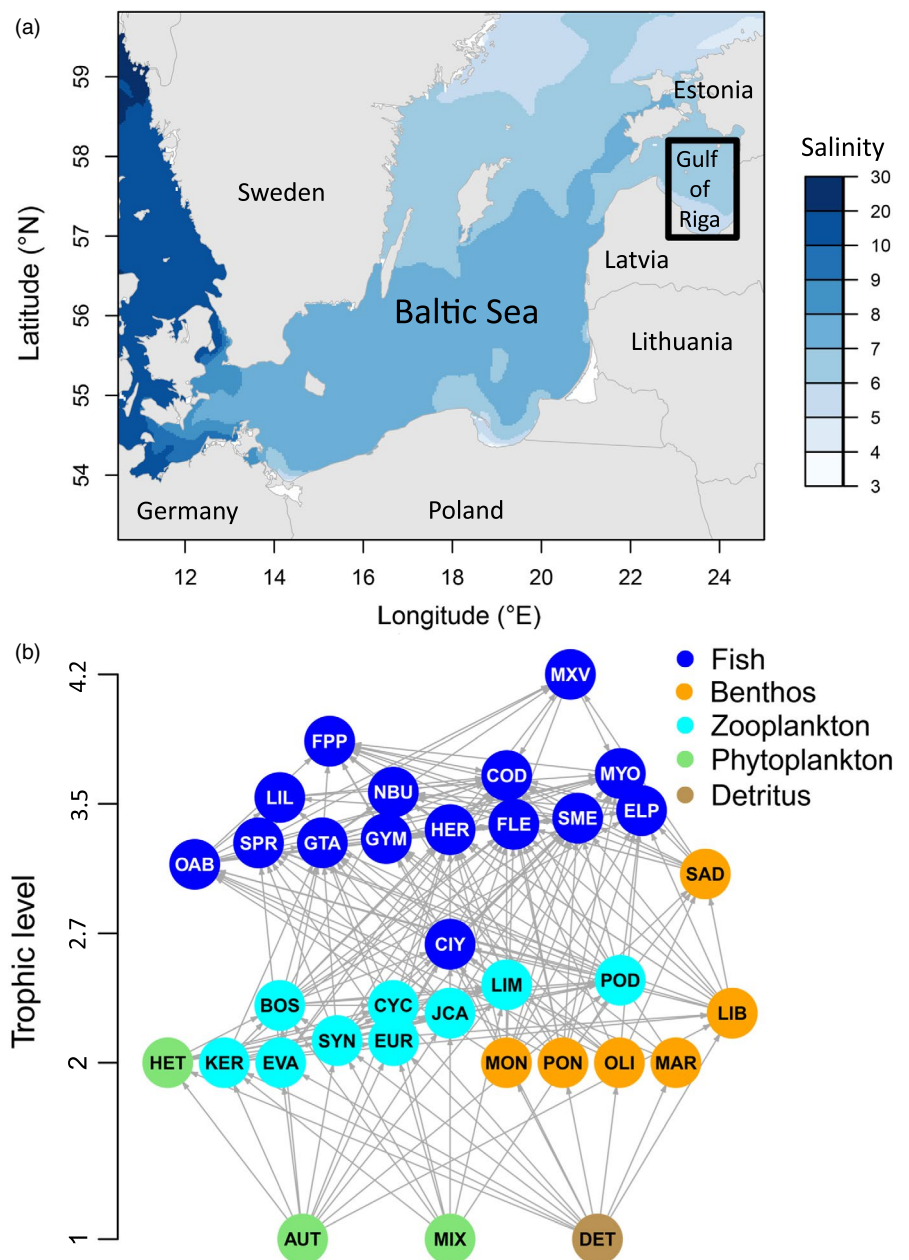
FIGURE 1 (a) Map of the southern and central Baltic Sea with salinity gradient in blue shadings. The Gulf of Riga study area is marked with a black rectangle. (b) The Gulf of Riga food web metaweb. Node labels are taxons' name abbreviations and correspond to the first three letters in a taxon's scientific name, except for fish, which follow the three-letter ASFIS standard: http://www.fao.org/fishery/collection/asfis/en. Node colours correspond to a taxon's main functional grouping. The full name of each taxon can be found in Appendix S2: Table S1

a permanent halocline (Kotta et al., 2008). Due to its shallowness, the dynamics of both surface and deep-water temperatures are coupled with air temperatures. High nutrient inputs result in high primary productivity (Rönnberg & Bonsdorff, 2004; Wasmund et al., 2011). However, the diversity of benthic invertebrates is low due to uniformity of the habitat and low salinity levels (Kotta et al., 2009). Herring strongly dominates the fish community, accounting for about 90% of the fish catches in the area (Ojaveer et al., 1999).

2.2 | Biomonitoring data

Species occurrence and biomass were used to construct a metaweb (Figure 1b). A metaweb is a compilation of species and their potential feeding interactions within a specific geographical area and time period, but does not represent observed realisations of trophic interactions at a given time step. Time-series data were obtained over a 38-year period from 1979 to 2016 for phytoplankton, zooplankton, benthos and fish. To respect species' seasonality and habitat dependencies, only monitoring surveys carried out in spring/early summer (May and June) at sampling stations deeper than 20 m (i.e. offshore communities) were considered for the analyses. Maps with sampling stations can be found in Appendix S1: Figure S1. No long-term time series were available for seals and seabirds; therefore, these groups could not be included in the food web analyses. As both seals and seabirds mostly prey on coastal fish communities (Hansson et al., 2017), we assume that their impact is limited on offshore community dynamics. However, we acknowledge that their exclusion likely reduces the number of trophic levels and mean path length of the food web (Blanchet et al., 2019).

2.3 | Subsampling core taxa for the metaweb

Only the most persistent and/or abundant taxa (i.e. the core taxa) over the 38 years were included in the metaweb (Appendix S2: Table S1). Persistence of a taxon was determined by identifying the inflection point of a third-order polynomial (i.e. sigmoid curve) fitted between the log total biomass and the number of years a species was present in the time series (Genner et al., 2004; Magurran & Handerson, 2003; Appendix S2: Figure S1). The value on the x-axis (i.e. the abscissa) of the inflection point separates the persistent from the less persistent taxa, resulting in a list of commonly reported taxa during the 38-year study period. The persistence analyses were complemented with an abundance threshold (the ordinate, i.e. the value on the y-axis of the inflection point) allowing the inclusion of not only persistent but also highly abundant species. These criteria were applied only, and separately, for fish and zooplankton datasets. Core fish and zooplankton taxa accounted for >99% and 93% of the total species biomass per group respectively. Conversely, all benthic invertebrate taxa were included, except Polychaeta, an aggregated group only recorded once. All phytoplankton taxa (i.e.

unicellular organisms) were included in the analyses, except the ciliate *Mesodinium* sp. due to lack of long-term data for this genus. Phytoplankton taxa were aggregated into three main groups: auto-, hetero- and mixo-trophs. Furthermore, we included the invasive, non-indigenous fish, round goby *Neogobius melanostomus*, which has become widespread in the Gulf of Riga with likely major ecological impact (Oesterwind et al., 2017). For each taxon, biomass (gram wet weight per m^2) per time step was calculated (Appendix S3: Figures S1–S5). The trophic links among the subsampled species in the metaweb were compiled by an extensive literature review on species gut content analyses primarily from the Baltic Sea. For more details on the construction of the metaweb, see Appendix S4.

2.4 | Temporal food webs

To study how food web structure in the Gulf of Riga varied through time, we built yearly snapshot food webs, representative of offshore communities in spring. For each year, a list of species was computed based on long-term biomonitoring data. This list was used to subsample trophic interactions from a metaweb (Kortsch et al., 2018). Because sampling effort varied between years among taxonomic groups (Appendix S1: Figure S2), we standardised the number of samples over the 38-year study period. Standardisation was performed by randomly selecting a fixed number of stations for each taxonomic group (5 stations for phytoplankton, 35 for zooplankton, 1 for benthos and 8 for fish) within 5-year moving windows. Although taxonomic groups were sampled with an uneven number of stations (Appendix S1: Figure S2), we did not adjust for this, because we aimed at using as much data (i.e. information) as possible. The 5-year moving window was applied to create a continuous time series with a constant number of samples for each time step. This resulted in new time series spanning from 1981 to 2014, where a 'year' represents the middle of a 5-year window, for example the average biomass and the frequency of occurrence of a taxon in 1981 is based on a fixed number of samples between 1979 and 1983 (Appendix S3: Figures S5 and S6). This standardised sampling procedure was iterated 1,000 times for each year, resulting in 1,000 assembled food webs per year. Strengths and limitations of constructing a metaweb, and using it to subsample temporal food webs, is discussed in Appendix S4.

2.5 | Fluxes

Using a bioenergetic food web approach (Barnes et al., 2018; Gauzens et al., 2019), we assigned weights (or energy fluxes) to the trophic links (Appendix S5: Figure S1). This approach takes advantage of allometric scaling laws to quantify metabolic rates (Brown et al., 2004). These metabolic rates together with losses to predation and assimilation efficiencies (i.e. the proportion of ingested food actually available for metabolism and growth) are used to quantify energetic fluxes in and out of each node. Metabolic rates per unit biomass (i.e. per gram) were multiplied with taxon-specific biomass

to achieve node-metabolic (or population-level metabolic) losses. Assuming system equilibrium, the model calculates energy fluxes in a top-down manner, which implies that each species' losses to predation and metabolism are balanced by its energetic gains defined as in-going fluxes multiplied by assimilation efficiencies (Barnes et al., 2018). In practice, this means that fluxes at the top of the food web are calculated first, where losses to predation are equal to zero, then fluxes at lower trophic levels are calculated based on the losses to consumers at higher trophic levels, and so on. The magnitude of fluxes are also dependent on consumers' diet preferences. In this study, preferences were based on the 'neutral assumption' that consumers feed the most on their most available prey, that is, the prey with the highest biomass (Gauzens et al., 2019). We acknowledge that this assumption can lead to under- or over-estimation of certain energetic fluxes among taxa. To account for differences in resource quality, the assimilation efficiencies were defined depending on prey type. Body mass estimates for fish, benthos and phytoplankton are specific for Gulf of Riga communities and derived from local biomonitoring data, except zooplankton body mass estimates which come from other areas within the Baltic Sea. All input parameters (Appendix S5: Table S1), including species-specific body masses and a description of and the equations to calculate the fluxes can be found in Appendix S5.

2.6 | Metrics of food web structure and function

To characterise the temporal structure of Gulf of Riga food webs, we selected seven unweighted, topology-based metrics (i.e. number of species, connectance, generality, vulnerability, shortest path length, short-weighted trophic level and degree of omnivory), and seven weighted metrics (i.e. four node-weighted: connectance, generality, vulnerability and trophic level, and three link-weighted: connectance, generality and vulnerability; Table 1). The selected food web metrics were chosen because they cover diverse and ecologically relevant aspects of food web structure (Table 1, and Appendix S6: Table S1), for example, they relate to the vertical (trophic level, omnivory) and the horizontal (generality, vulnerability) dimensions of food webs and to their complexity (species richness, connectance).

To compute link-weighted metrics we used the estimated energy fluxes following the approach of Bersier et al., (2002). The link-weighted metrics were calculated by estimating the average effective number of prey and predators of each taxon weighted by their relative in- and out-flows. First, the effective number of prey and predators was calculated by applying the Shannon's index to each taxon's in- and out-flows (Bersier et al., 2002; Shannon, 1948; Ulanowicz & Wolff, 1991), next, the energetic and functional importance of

TABLE 1 Assumptions, advantages and limitations of the unweighted and weighted food web approaches used to describe food web structure in this study

Approaches	Metrics	Abbreviations	Assumptions	Advantages	Limitations
Unweighted	Number of species	S	Networks are binary and based on species presence/absence. Species and trophic links are weighted equally	A binary food web is relatively easy to construct without strong assumptions on biomasses of species, and energy fluxes between species Roles of species can easily be determined from their network position	Rare and unimportant species in terms of energy fluxes influence food web structure to the same degree as dominant and/or functionally important species. Ignores the asymmetry of fluxes among taxa, which may overestimate structural properties
	Connectance	C			
	Generality	G			
	Vulnerability	V			
	Shortest path	ShortPath			
	Short-weighted trophic level	TL			
	Level of omnivory	Omni			
Node-weighted	Connectance	nwC	Trophic species (i.e. nodes) are weighted by their biomass; hence, nodes with high biomass will have a stronger influence on structural properties	Node-weighted metrics can identify dominant species and alterations in dominance related to changes in species' biomass structure	Species' dominance does not equal functional importance in the network It is hard to harmonise biomass data across trophic groups (e.g. sessile benthos and free-swimming fish), or to assess biomass for a non-sampled node (e.g. detritus)
	Generality	nwG			
	Vulnerability	nwV			
	Trophic level	nwTL			
Link-weighted	Connectance	lwC	Edges (or links) are proportional to the magnitude of energy fluxes, taking into account that some fluxes (links) are stronger than others	Takes the magnitude, diversity, and the distribution of energy flows into account, and allows the calculation of species effective number of prey and predators. Assessing the magnitude of fluxes can inform about functioning and stability of the system	The bioenergetic model applied assumes a steady state. Unless prey preferences are defined, the model assumes that prey items with highest biomass will be the most important prey of a consumer, which may lead to under- or over-estimation of some fluxes
	Generality	lwG			
	Vulnerability	lwV			

each taxon was assessed by weighting the effective number of prey and predators by their in- and out-flows over the total flow. Energy fluxes among taxa were also used to quantify functions. We considered five functions: detritivory, phytoplanktivory, zooplanktivory, benthivory and piscivory, which are calculated as the sum of fluxes from detritus, phytoplankton, zooplankton, benthos and fish to their consumers respectively. Here, we present the relative contribution of each function as a percentage of the total flux in the networks for each year.

Another way to consider the effect of changes in species' biomass on food web structure is through node-weighted metrics (Olivier et al., 2019). Under this framework, a species biomass is used to assess the importance of its contribution to a network descriptor. For instance, the node-weighted trophic level of a food web will correspond to the average of species' trophic levels weighted by their biomass. These node-weighted metrics capture changes in food web structure caused by alterations in species' relative biomass structure and dominance patterns, without making further assumptions about the dynamics of energy fluxes.

For each time step, each metric and function was computed for the 1,000 assembled food webs, and its temporal dynamics depicted as medians with confidence intervals over the 1,000 repetitions. Different food web approaches (unweighted and weighted) come with their own set of advantages and limitations, briefly outlined in Table 1. A short description of each metric including its mathematical notation can be found in Appendix S6: Table S1.

2.7 | Numerical and statistical analyses

To assess how food web structure and function varied during the study period (research question a), we plotted each metric and function with median values and corresponding confidence intervals based on the 1,000 assembled food webs. Then, we performed a multivariate principal component analysis (PCA) on the median values to investigate the main temporal dynamics in food web structure and function, and to assess whether unweighted and weighted food web approaches highlight different (or similar) aspects of temporal food web dynamics (research question b). Finally, a cluster analysis on the main temporal dynamics (i.e. the year scores of the PC1 and PC2) was performed to identify periods with distinct food web properties and functions (research question c).

A PCA identifies the main dynamics in food web structure and function with a few dimensions, called principal components (PCs). Each metric contributes with a different weight (i.e. absolute loading) to the PCs. Contributions of the different food web approaches to the PCs were depicted in bar plots. Another way to visualise the main temporal trends in metrics is by sorting the metrics according to their loadings on PC1 and PC2 in heatmaps (Diekmann et al., 2012, see Appendix 7: Figure S1). Furthermore, the year scores of PC1 and PC2 were used to identify groups of years (i.e. periods) with similar food web characteristics by applying a constrained hierarchical clustering on the food web time series (Appendix S8: Figure S1), using

Euclidean distances and agglomeration based on incremental sum of squares (Grimm, 1987), which forces the solution to be chronologically consistent. Empirical values per food web period and associated biological changes were summarised in two tables respectively (Appendix S8: Tables S1 and S2). Weighted food webs per period were illustrated, where edge (i.e. link) weights equal the average link weight over a period.

All computations and statistical analyses were performed in R version 3.6.1 (R Development Core Team, 2019) using custom-written code and available R packages. Several of the food web metrics including the food web graph were performed using the IGRAPH package (Csardi & Nepusz, 2006). Fluxes were calculated using the FLUXWEB package (Gauzens et al., 2019). The multivariate analyses, PCA and constrained hierarchical clustering, were performed with the statistical packages ADE4 (Dray & Dufour, 2007) and RIOJA (Juggins, 2020) respectively.

3 | RESULTS

The univariate food web time series show substantial temporal variability in unweighted and weighted food web metrics and flux-based functions over the 34-year study period (Figure 2). The trajectories of the univariate food web time series show that the temporal dynamics among approaches vary. For example, different types of network connectance (i.e. unweighted, node- and link-weighted) display distinct variability and complementary dynamics. Unweighted connectance (C) is highest at the beginning of the time series (C = 21.5% in 1997) until 1998, after which it drops abruptly (C = 17.7% in 2001). Node-weighted connectance (nwC) decreases throughout the time series (from nwC = 21.5% in 1983 to nwC = 17.8% in 2014), but peaks with highest values in the mid-1990s (in 1993–1995, nwC > 23%). In contrast, link-weighted connectance (lwC) displays relatively high values in the years 1994–2001 and 2009–2013 (lwC > 10%) compared to other years with lwC ~ 8%. Generally, link-weighted metrics have lower values than the unweighted topology-based metrics.

The PCA captures the relationship and associations in the dynamics among metrics over the study period. The first two principal components (i.e. PC1 and PC2) account for 64% of the variability in temporal food web dynamics, 37% and 27% respectively (Figure 3a). The contribution bar plots show that weighted metrics and functions (except percentage benthivory) contribute strongly (89%) to the variability in food web dynamics captured by PC1, whereas unweighted metrics (except omnivory) contribute (44%) the most to the variability captured by PC2 (Figure 3b). Node-weighted vulnerability, degree of omnivory and proportion of detritivorous flows are negatively associated with PC1, whereas node-weighted generality, link-weighted connectance, link-weighted vulnerability and link-weighted generality, and proportion of phytoplanktivorous and zooplanktivorous flows is positively associated with PC1 (Figure 3a, Appendix S7: Figure S1a). Metrics negatively associated with PC2 include number of species, generality, vulnerability and
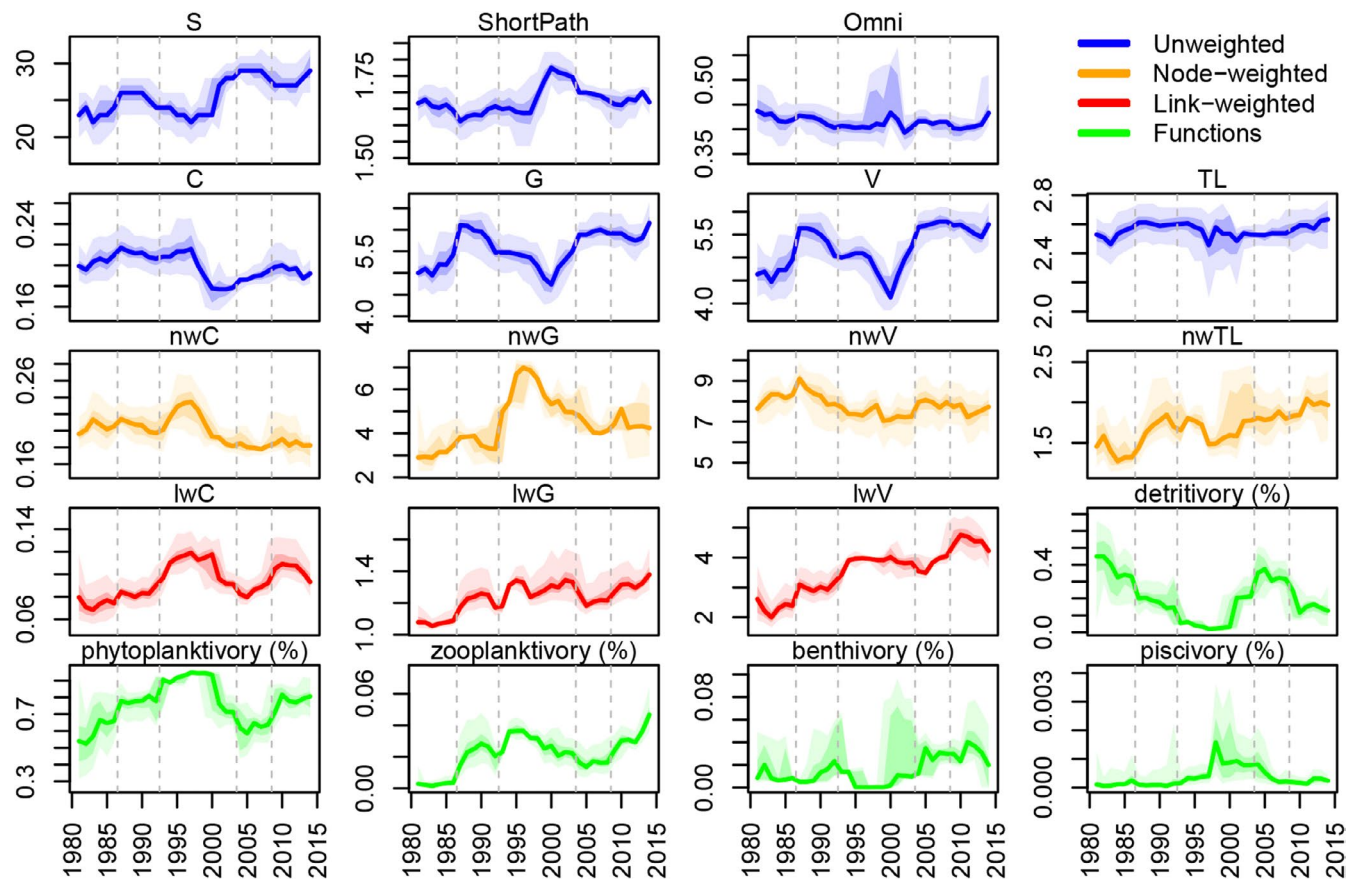
FIGURE 2 Time series of unweighted and weighted food web metrics, including flux-based functions, over a 34-year study period (1981–2014) in the Gulf of Riga. The bold lines are the median values with corresponding 50% and 95% confidence intervals (coloured shaded areas). The metrics are coloured according to approach: unweighted (blue), node-weighted (orange) and link-weighted (red). Time series of functions are depicted as percentages (green), note that the scale on the y-axes are not the same among functions. Panel titles correspond to unweighted and weighted metric abbreviations; see full name of each metric in Table 1

percentage benthivorous flows, whereas node-weighted connectance is positively associated with PC2 (Figure 3a, Appendix S7: Figure S1b).

Constrained hierarchical clustering of the year scores on PC1 and PC2 (Appendix S8: Figure S1) revealed five periods with distinct food web characteristics: 1981–1986, 1987–1992, 1993–2003, 2004–2008 and 2009–2014 (Figure 3a,c). The first period (i.e. 1981–1986) was characterised by relatively low values in topology-based metrics, such as species number, vulnerability and generality and low values in link-weighted metrics—indicating low evenness of fluxes (i.e. also low weighted network complexity), whereas the percentage of detritivorous flow was highest in the first period (Figure 2, Appendix S8: Table S1). Two phytoplankton groups (auto- and heterotrophs), two zoobenthos taxa (the amphipod *Monoporeia affinis* and Oligochaeta) and cod *Gadus morhua*, had high biomasses, whereas pelagic fish species such as herring *Clupea harengus* had low biomass (Appendix S3: Figures S1, S3 and S4; Appendix S8: Table S2). In the second period (1987–1992), herring and some zooplankton biomass (*Evadne* spp., *Keratella* spp., *Podon/Pleopis* spp. and *Synchaeta* spp.) increased substantially, increasing the zooplanktivorous and phytoplanktivorous flows. The period from 1987 to 1992 can be regarded as a

transition period from relatively high detritivorous flows (1981–1986) to a food web period dominated by planktivorous flows (1993–2003).

The third period, 1993–2003, is characterised by dominance of pelagic processes, that is, phytoplanktivorous (87%) and zooplanktivorous flows, and by relatively high values in node-weighted generality (Figure 2, Appendix S8: Table S1). In terms of biomass structure, this period is characterised by major decreases in zoobenthos and high biomass of herring (Appendix S8: Table S2). Despite the fact that food webs in period one (1981–1986) and three (1994–2003) display large differences in terms of functions (detritivore- vs. pelagic-dominated fluxes), they are relatively similar with respect to topology-based metrics (Appendix S8, Table S1). For example, mean number of species (~23), mean connectance (~20%), mean vulnerability (~4.7) and mean generality (~5.2) display almost the same values between these periods.

The two last periods (i.e. 2003–2008 and 2009–2014) were characterised by the highest values in species number, node-weighted trophic level and high benthivore fluxes, but lower node-weighted connectance (Figure 2, Appendix 8: Table S1). The last period (2009–2014) in particular is positively associated with high link-weighted vulnerability and generality. Generally, frequency of occurrence

FIGURE 3 (a) PCA biplot of metrics summarising the temporal dynamics in food web structure and flux-based function, shaded grey areas define the convex hull of the temporal clusters grouping years with similar food web characteristics. The arrow colours of the metrics represent different approaches: qualitative metrics (blue), node-weighted metrics (orange), link-weighted (red) and functions (green). (b) Percentage contribution of each food web approach to PC1 and PC2. Metric abbreviations are described in Table 1, except for the functions: detri = detritivory (%), benth = benthivory (%), phyto = phytoplanktivory (%), zoopl = zooplanktivory (%) and pisci = piscivory (%). (c) Illustrations of average link-weighted food webs for five time periods distinguished by hierarchical clustering: 1981–1986, 1987–1993, 1994–2003, 2004–2008 and 2009–2014. The width of the trophic links corresponds to the magnitude of energy fluxes

and biomasses of several taxa across functional groups increased in the 2000s. For example, pelagic fish species such as three-spined stickleback *Gasterosteus aculeatus* and sprat *Sprattus sprattus*, and benthivorous fish species such as snailfish *Liparis liparis* and sculpin *Myoxocephalus quadricornis* all had high biomasses (Appendix S3: Figure S4 and Appendix S8: Table S2). Also several small-sized zooplankton taxa increased, such as the copepods *Eurytemora affinis*,

Acartia spp., Cyclopoida and the cladocerans *Bosmina* spp. and *Evadne* spp., as well as the benthic amphipod *Pontoporeia femorata* and isopod predator *Saduria entomon* (Appendix S3: Figures S2 and S3). The non-indigenous species round goby *N. melanostomus* appeared in our samples during the last time period, while the biomass of the non-indigenous, invasive polychaete *Marenzelleria* spp. increased substantially in the 2000s (Appendix S3: Figures S2 and S4).

4 | DISCUSSION

Applying unweighted and weighted approaches to long-term food web time series allowed us to assess food web structure and function, and to reveal complementary patterns of change and variability in food web dynamics, likely reflecting different ecosystem processes. The observed temporal variability in food web structure and function, and the complementarity among approaches, demonstrates the benefit of using a combination of topology-, biomass- and flux-based food web metrics to draw a more complete picture of temporal ecosystem dynamics. In fact, some of the observed ecosystem changes, and the nature of these changes, would not have been easily detected using only a single approach. Furthermore, by comparing food web structure and function, our study indicates that changes in ecosystem functioning over time cannot be predicted using unweighted food web metrics, such as species number, but rather should be assessed through the lens of energy flux distributions.

Analyses of the food web time series revealed five periods with distinct food web characteristics in the Gulf of Riga, separated by pronounced changes in unweighted and weighted network properties. The first two discernible changes, occurring in 1986/87 and 1992/93, were characterised by decreases in detritivorous flows, and increases in pelagic flows. The in-between years (1987–1993) may be regarded as a possible transition period, as pointed out in a previous study on regime shifts in the Baltic Sea (Möllmann et al., 2009). Reflected as alterations in energy fluxes, our study confirms the previously documented multi-trophic reorganisations in species community structure and trait composition in the Gulf of Riga at the end of the 1980s (Casini et al., 2012; Pecuchet, Lindegren, et al., 2020). Likely explanations for the changes in food web functions (i.e. decreases in detritivorous and increases in phyto- and zooplanktivorous fluxes) are alterations in community structure as a response to changes in abiotic drivers, such as increases in temperature during the specific time periods.

In the early 1980s, the Gulf of Riga was characterised by a relatively cold climate and ice cover during winters (Einberg et al., 2019; Ojaveer et al., 1999), favouring cold-water relict species such as Arctic diatoms (Jurgensone et al., 2011), and benthic crustaceans *M. affinis* and *Limnocalanus macrurus*. We conjecture that the high benthic biomass and detritivorous flows at the beginning of the time series can have been promoted by the sinking out of lipid-rich diatoms to the seafloor, entering the detritus pool and thus serving as fuel for benthic biomass production. In contrast, the milder winters in the 1990s with no ice formation likely favoured growth of warm-water zooplankton species such as the rotifer *Keratella* spp., the cladoceran *Bosmina* spp. and the copepod *Eurytemora affinis* (Livdāne et al., 2016), as well as reproduction and growth of herring (Ojaveer et al., 1999). Increases in these pelagic taxa may have enhanced processes leading to high phyto- and zooplanktivorous flows. At the same time, the low benthic biomass during the 1990s further reduced detritivorous flows. Despite large differences in functions between the first (1981–1986) and third (1993–2003) time period,

the topology-based metrics are relatively similar. This suggests that topological metrics are inadequate predictors of ecosystem functioning, as they cannot capture the subtle fluctuations in species dynamics and associated consequences for energy flux distributions.

Although topology-based metrics are inadequate at capturing processes related to ecosystem functioning, they are useful for assessing compositional changes in the network structure related to increases in species and link richness. For example, the sudden increase in species number around the year 2,000 mirrors observed trends of increasing species richness in the neighbouring Baltic Proper (Bergström et al., 2015; Törnroos et al., 2019). Species increasing in number include pelagic fish species (e.g. sprat and sticklebacks), zooplankton species (e.g. *Eurytemora affinis*, *Acartia* spp.) and benthos (e.g. *Pontoporeia femorata*), as well as two non-indigenous species (*Marenzelleria* spp. and round goby). These compositional changes, and associated food web changes (e.g. increases in species richness, vulnerability and generality), can be linked to large-scale processes driven by anthropogenic pressures in the Baltic Sea during the 2000s (Reusch et al., 2018). Increases in seawater temperatures due to climate warming may favour reproduction in some pelagic species, such as sticklebacks (Bergström et al., 2015), whereas increases in maritime transport facilitates the introduction of new, non-indigenous species (Ojaveer et al., 2017).

Applying unweighted and weighted metrics enabled us to gain complementary insights into the dynamics of Gulf of Riga food webs. Unweighted, node- and link-weighted metrics displayed substantial variability throughout the study period, but with distinct dynamics and trends. For example, unweighted connectance is relatively constant (or invariant) until the year 2000, after which it suddenly decreases. This decline is linked to increases in the number of possible interactions without significant increases in the mean number interactions per taxon, and primarily reflects the increase in species number. Therefore, viewed through the lens of temporally resolved food webs, our findings do not support the original constant connectance hypothesis, which states that on average a fixed fraction of all possible links are realised independent of the number of species in the community (Martinez, 1992). Node-weighted connectance is highest in the mid-90s, which can be explained by high biomass of highly connected nodes, such as herring, combined with low species number, reflecting the dominance of particular taxa in the food web during these years. Link-weighted connectance (weighted complexity), which reflects the effective connectance of the network, shows highest values in the middle (1993–2003) and last period (2009–2014). High values in link-weighted connectance indicates that several taxa with many interactions also have relatively high and even in- and out-flows (i.e. high effective number of links), which increases link-weighted food web complexity. Generally, link-weighted metrics have lower values compared to their unweighted counterparts, which indicates that flows are not equally distributed in food webs, but rather skewed towards a few strong and many weak fluxes. This calls for the inclusion of weighted networks (e.g. flux-based) to obtain more realistic assessments of structural and functional food web changes.

Unweighted and weighted food web approaches highlight different and complementary facets of change at the ecosystem level, suggesting that there is no primacy of using one approach over the other. Rather, it is their combined assessment that provides the most complete insights into ecosystem changes (see also Banašek-Richter et al., 2009; Bersier et al., 2002), a finding which has implications for the nature of food web inquiry. If the research goal is to assess major structural food web reorganisations without complete loss or gain of species and without substantial link rewiring, then the binary food web structure may appear unchanged, despite the fact that weighted food web structure and ecosystem functioning may have changed considerably. For example, in a review paper on temporal food webs, it was concluded that macroscopic food web descriptors, such as unweighted connectance, generally, seem invariant at a wide range of temporal scales, spanning years to millennia (Trøjelsgaard & Olesen, 2016). This finding is not evident in our analyses, as we observe substantial variability in both unweighted and weighted macroscopic network descriptors over the course of our 34-year study period.

The suggested invariance of macro-descriptors in food web studies (Trøjelsgaard & Olesen, 2016), which are primarily based on unweighted networks, may lead to the conclusion that either no ecosystem shifts have occurred, or that food web structure is resilient to environmental changes (Griffith et al., 2019; Yletyinen et al., 2016), or that food web structure requires severe biotic and/or abiotic shifts to change (Trøjelsegaard & Olesen, 2016). Neither of these may hold true if weighted food web structure had been considered, taking into account the subtle changes in species' population dynamics. Based on the results of our study, we therefore recommend employing a range of descriptors from both unweighted and weighted food web approaches in order to characterise the dynamic and multifaceted nature of structural and functional ecosystem changes. Moreover, the mechanisms that give rise to the differences in unweighted and weighted food web properties are not necessarily related to the same ecosystem processes (e.g. dispersal and invasion, population dynamics or climate variability etc.; Maureaud et al., 2020). Along these lines, it should be carefully considered, a priori as well as a posteriori, whether the observed empirical changes are related to alterations in species composition, community structure, dominance patterns, energetic fluxes or a combination of these. It is also important to consider whether an unweighted or weighted food web approach is appropriate to tackle a proposed research objective. Ignoring these details may possibly lead to incorrect conclusions about the nature of the ecosystem changes at varying temporal scales.

5 | CONCLUSIONS

We found marked temporal change and variability in Gulf of Riga food web structure and function using unweighted and weighted metrics. The temporal dynamics in food web structure differed between approaches. Not surprisingly, unweighted, topology-based metrics performed better at capturing changes related to species and link richness, whereas weighted metrics were better at capturing fluctuations related to species population dynamics and biomass structure. Reflected in the flux distributions, our study corroborates the previously documented reorganisations in the Gulf of Riga at the end of the 1980s, and thus demonstrates how shifts in food web structure can manifest as changes in ecosystem functioning. However, this shift in functioning could only be assessed by comparing food web structure and functions using a flux-based approach. The full extent of the food web changes reported in this study was only possible because of the complementarity between unweighted and weighted food web network approaches. Therefore, we argue that there is no primacy of using one approach over the other; rather, it is the combined assessment that provides the fullest insights into the different changes occurring in an ecosystem. Yet, in order to capture the subtle fluctuations in species population dynamics and its effects on ecosystem functioning, the inclusion of a flux-based approach and weighted networks is recommended.

AUTHORS' CONTRIBUTIONS

S.K., R.F. and M.C.N. conceived the study; S.K. and R.F. contributed equally to the design, analyses and interpretation of the results; R.F. prepared the figures; I.J., S.S., G.R., E.K., S.K., P.O., L.P., H.O. and I.P. collected and compiled the data; S.K. wrote the first draft of the manuscript. All authors contributed with ideas for the interpretation of the data and with inputs to the manuscript. All authors gave their final approval for publication.

DATA AVAILABILITY STATEMENT

The Gulf of Riga metaweb food web, that is, the pairwise trophic interaction list including references, as well as body mass of each taxon including references, is available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.6t1g1jwwn (Kortsch et al., 2021). An R script tutorial to perform the food web analyses on the metaweb is available through GitHub: https://rfrelat.github.io/BalticFoodWeb.html via: https://doi.org/10.5281/zenodo.3902039 (Kortsch et al., 2020).

ORCID

Susanne Kortsch (iD) https://orcid.org/0000-0002-6495-4781
Romain Frelat (iD) https://orcid.org/0000-0002-8631-4398
Laurene Pecuchet (iD) https://orcid.org/0000-0002-8930-8786
Ivars Putnis (iD) https://orcid.org/0000-0003-3323-6135
Erik Bonsdorff (iD) https://orcid.org/0000-0001-5070-4880
Henn Ojaveer (iD) https://orcid.org/0000-0003-2742-6063
Iveta Jurgensone (iD) https://orcid.org/0000-0002-0811-1747
Solvita Strāķe (iD) https://orcid.org/0000-0002-0537-3303
Marie C. Nordström (iD) https://orcid.org/0000-0001-5763-1813

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.