

**Pierre Olivier**

# **Marine Food Webs:**

an Exploration of Past Structure and Function  
to Prepare for the Future





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Cover image by Anna Laurine Kornum



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an Exploration of Past Structure and Function  
to Prepare for the Future

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Following my dreams of Ocean, or an ocean of dreams.

*“Our past, our present, and whatever remains of our future, absolutely depend on what we do now. With every drop of water you drink, every breath you take, you’re connected to the sea. No matter where on Earth you live.”*

— Sylvia Earle

My thesis is dedicated to my grandma, Mathilde, who left us before to see its completion. You always supported me, no matter what choices I would make, because those choices—victories or mistakes—would solely be mine. You always understood that for me the sea was everything, and that I would fight for my dreams. For that, I will forever be grateful and will continue to fight for my dreams, whatever they will be, and wherever they will take me.

Ma thèse est dédiée à ma grand-mère, Mathilde, qui nous a quittée avant d’en voir son achèvement. Tu m’as toujours encouragé, peu importe mes choix, bons ou mauvais, parce que ces choix m'appartiennent. Tu as toujours compris ma passion pour la mer et que je n’en démordrai pas. Pour ça, je t’en serais éternellement reconnaissant et continuerai de me battre pour mes rêves, peu importe ce qu’ils seront ou me mèneront.



# ABSTRACT

Food webs depict species and their trophic interactions arranged in a network. Changes in food web structure ultimately beget changes in functioning. In recent years, environmental and anthropogenic pressures have reshaped marine communities beyond recognition, with either gains (e.g. through invasions) or losses (e.g. through local extinctions) in biodiversity. Still, we do not know how it has impacted the food web. Assessing changes in the structure and function of food webs is complex as the components at the core of food webs (the composition of species and the architecture of trophic interactions) can vary in intricate ways. As a result, sampling temporally resolved food webs is often difficult and, consequently, few studies have investigated temporal changes in structure and function. The few studies available have often relied on data with low temporal resolution (such as, a before-and-after state). To study temporal variation in food web structure, we need to improve how we build networks, and develop a framework that allows us to identify diverse changes in food webs over time.

The overall aim of this thesis is two-fold. First, the thesis explores temporal changes in food web structure and function, and aims at disentangling changes that originate from shifts in species composition, dominance of species (abundance, biomass), trophic links (caused by changes in composition), as well as energy fluxes. In **Paper I** and **II**, I constructed time series of food web metrics for two local food webs (the German Bight in the North Sea and the Gulf of Riga in the Baltic Sea), including metrics developed to identify topological changes occurring without the complete loss of species. I built yearly snapshots of food webs by subsampling taxa and their trophic links from metawebs (a food web topology that contains all possible species and trophic interactions) using time series of species abundances or biomasses. The findings highlight that temporal changes in food webs are complex and varied: study of food web temporal development necessitates the use of complementary metrics that integrate and expose the various underlying causes of change (e.g. species composition, dominance, trophic interactions, energy fluxes). For instance, variation in food web structure resulting from changes in species composition may further impact the functioning of the food web, and simultaneous assessment of both types of changes is possible using a set of complementary qualitative and quantitative food web metrics.

Second, I aim to find new ways to improve the building, use, and applicability of food webs. Being able to build realistic food webs is essential if we want to study their structure and functioning, or integrate food webs into monitoring and management of ecosystems. Future advances require tackling fundamental challenges: how to aggregate species and their links when diet data is scarce; or which trophic links to include, for instance, when species composition changes over time. In **Paper III**, I tested the sensitivity of food web structural metrics to

several aggregation procedures. I show that metrics differ in their sensitivity to aggregation, and that not all aggregation methodologies perform best at maintaining food web structure. In **Paper IV**, I investigated trait-associations through which consumers and resources interact at the local scale. Functional traits of species govern where species live and with whom they can interact. I found that food webs structure along a continuum determined by similarities in habitat characteristics, where species in similar habitats most likely share traits. By combining food webs and traits, I identified trait profiles that portray interacting consumers and resources along the basic vertical organization of food webs (trophic levels). Trait profiles characterise interacting consumers and resources, and can thereby help with inference of trophic interactions for the purpose of building food webs.

**Keywords:** food web, coastal community, environmental changes, time series, food web aggregation, functional traits, trait matching, bipartite network.

Turku, December 24th, 2021

*Pierre Olivier*



# SAMMANFATTNING

Näringsväven skildrar arter och deras trofiska interaktioner ordnade i ett nätverk. Förändringar i näringsvävens struktur kan leda till förändringar i dess funktion. Under de senaste åren har miljömässiga och människorelaterade belastningar omformat marina samhällen till oigenkännlighet, med antingen vinster (t.ex. genom invasioner) eller förluster (t.ex. genom lokala utrotningar) i biologisk mångfald. Ändå vet vi inte hur detta påverkat näringsväven. Att utvärdera förändringar i näringsvävarnas struktur och funktion är komplicerat eftersom komponenterna i kärnan av näringsväv (artsammansättningen och de trofiska interaktionernas arkitektur) kan variera på invecklade sätt. Därmed är provtagning av tidsmässigt detaljerade näringsvävar ofta svårt och följaktligen har få studier undersökt tidsmässiga förändringar i deras struktur och funktion. De få tillgängliga studierna har ofta förlitat sig på data med låg tidsupplösning (t.ex. jämförelse av före och efter). För att studera tidsmässig variation i näringsvävens struktur måste vi förbättra hur vi bygger nätverk och utveckla ett ramverk som gör att vi kan identifiera olika förändringar i näringsväven över tid.

Avhandlingens övergripande syfte är tvådelat. För det första utforskas tidsmässiga förändringar i näringsvävens struktur och funktion, med avsikt att klargöra förändringar som härstammar från ändringar i artsammansättning, dominans av arter (förekomst, biomassa), trofiska länkar (orsakade av förändringar i sammansättning) och energiflöden. I **Artikel I och II** sammanställde jag tidsserier av beskrivande variabler för näringsvävar i två områden (Tyska bukten i Nordsjön och Rigabukten i Östersjön). Dessa inkluderade mått som utvecklats för att identifiera topologiska förändringar som inträffar utan fullständig förlust av arter. Jag byggde årliga ögonblicksbilder av näringsvävarna genom att ta delprov av taxa och deras trofiska länkar från "metanätverk" (en näringsvävstopologi som innehåller områdets alla möjliga arter och trofiska interaktioner) med hjälp av tidsserier av arternas abundans eller biomassa. Resultaten framhäver att tidsmässiga förändringar i näringsväv är komplexa och varierande. Studier av näringsvävens tidsmässiga utveckling kräver därmed användning av komplementära mått som integrerar och skildrar de olika bakomliggande orsakerna till förändring (t.ex. artsammansättning, dominans, trofiska interaktioner, energiflöden). Variation i näringsvävens struktur till följd av förändringar i artsammansättningen kan till exempel ytterligare påverka näringsvävens funktion, och samtidig bedömning av båda typerna av förändringar är möjlig med hjälp av kompletterande kvalitativa och kvantitativa variabler.

För det andra strävar jag efter att hitta nya sätt att förbättra uppbyggnad, användning och tillämpbarhet av näringsvävar. Att kunna bygga realistiska näringsvävar är väsentligt om vi vill studera deras struktur och funktion, eller integrera näringsvävar i övervakning och förvaltning av ekosystem. Framtida framsteg kräver att man tacklar grundläggande utmaningar: hur arter och deras

interaktioner sammanslås när tillgängligt data är bristfälligt, eller vilka trofiska länkar som ska inkluderas, till exempel när artsammansättningen förändras över tiden. I **Artikel III** undersökte jag hur olika sammanslagningsmetoder påverkar näringsvävens struktur. Jag visar att måtten skiljer sig i sin känslighet, och att alla metoder inte fungerar väl för att upprätthålla strukturen i näringsväven. I **Artikel IV** undersökte jag egenskaperna som beskriver konsumenter och deras byten som växelverkar på lokalnivå. Funktionella egenskaper hos arter styr var arter lever och med vilka andra de kan interagera. Jag fann att näringsvävens struktur varierar längs ett kontinuum som bestäms av karakteristika för olika livsmiljöer, där arter i liknande livsmiljöer med största sannolikhet har lika egenskaper. Genom att kombinera näringsväven struktur med arternas funktionella egenskaper identifierade jag egenskapsprofiler som beskriver interaktioner mellan konsumenter och deras byten över trofiska nivåer. Egenskapsprofilerna beskriver konsumenter och deras byten och kan därmed underlätta härledning av trofiska interaktioner för sammanställning av näringsvävar.

**Nyckelord:** näringsväv, kustsamhälle, miljöförändringar, tidsserier, aggregering av näringsväv, funktionella egenskaper, matchande egenskaper, tvådelat nätverk.

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I	<b>Olivier, P.</b> , Frelat, R., Bonsdorff, E., Kortsch, S., Kröncke, I., Möllmann, C., Neumann, H., Sell, A.F. and Nordström, M.C., 2019. Exploring the temporal variability of a food web using long-term biomonitoring data. – Ecography 42, 2107–2121.
II	Kortsch, S., Frelat, R., Pecuchet, L., <b>Olivier, P.</b> , Putnis, I., Bonsdorff, E., Ojaveer, H., Jurgensone, I., Strāķe, S., Rubene, G., Krūze, Ē. and Nordström, M. C., 2021. Disentangling temporal food web dynamics facilitates understanding of ecosystem functioning. – J. Anim. Ecol. 90: 1205–1216.
III	<b>Olivier, P.</b> and Planque, B., 2017. Complexity and structural properties of food webs in the Barents Sea. – Oikos 126, 1339–1346.
IV	<b>Olivier, P.</b> , Lindegren, M., Bonsdorff, E. and Nordström, M. C. A network of biological traits: profiling consumer-resource interactions. Manuscript.

Author contributions to the individual papers

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Data collection	PO, BP	PO, IK, HN, AFS	IJ, SS, GR, EK, SK, PO, LP, HO, IP	PO
Data analysis	PO, BP	PO, RF	SK, RF	PO
Manuscript preparation	PO, BP	PO, RF, EB, SK, IK, CM, HN, AFS, MCN	SK, RF, LP, PO, IP, EB, HO, IJ, SS, GR, EK, MCN	PO, ML, EB, MCN

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# 1. INTRODUCTION

How nature, in all its complexity, is so well organized has puzzled scientists for centuries. Species come and go, join an ephemeral and intimate dance in which each and everyone of them finds a role. However, during the past decades, that complex organization has started to unravel: human-induced environmental threats have been rapidly disrupting this fragile equilibrium and reshaped the Earth's ecosystem so much that we may no longer be watching the same picture and may never solve the puzzle of life (Ceballos et al. 2015). Worldwide, species are forced on the move, expanding their geographical range or invading new territories (e.g. distributional shift of benthos, Weinert et al. 2016, northward migration of boreal species, Pecuchet et al. 2020a), or going locally extinct if they cannot adapt to new environmental conditions (Pimm et al. 2014, Young et al. 2016). Restriction or expansion of geographical range, invasion of new territories, or loss/removal of species from local communities often lead to a reorganization of local ecological communities. For instance, the introduction of the round goby in the Baltic Sea food web has brought new feeding opportunities for some species (e.g. perch, pike perch and cormorants) but also decreased resource availability and increased competition for food for others (e.g. with flounders, Oesterwind et al. 2017), with sometimes a significant niche overlap with other predators (e.g. with perch in terms of diet and habitat use, Herlevi et al. 2018). In other instances, species may be migrating to unexplored habitats and contributing to new ecological communities: in the Barents Sea, for example, *Gadus morhua*, cod, has been migrating poleward to avoid the warming of boreal waters (Kortsch et al. 2015). How the gains and losses of species have been affecting the structure and functioning of ecosystems through the food web is largely unknown because research has mainly focused on single trophic levels or functional groups (Duffy 2002, Eisenhauer et al. 2019). However, in nature, species are never alone, and changes in population dynamics of one species often impact others.

## 1.1. What are food webs and why study them?

### 1.1.1. Definition and brief history

*“Every animal is closely linked with a number of other animals living round it, and these relations in an animal community are largely food relations. [...] If we turned to the sea, or a fresh-water pond, or the inside of a horse, we should find similar communities of animals, and in every case we should notice that food is the factor which plays the biggest part in their lives, and that it forms the connecting link between members of the communities.” — (Elton, 1927)*

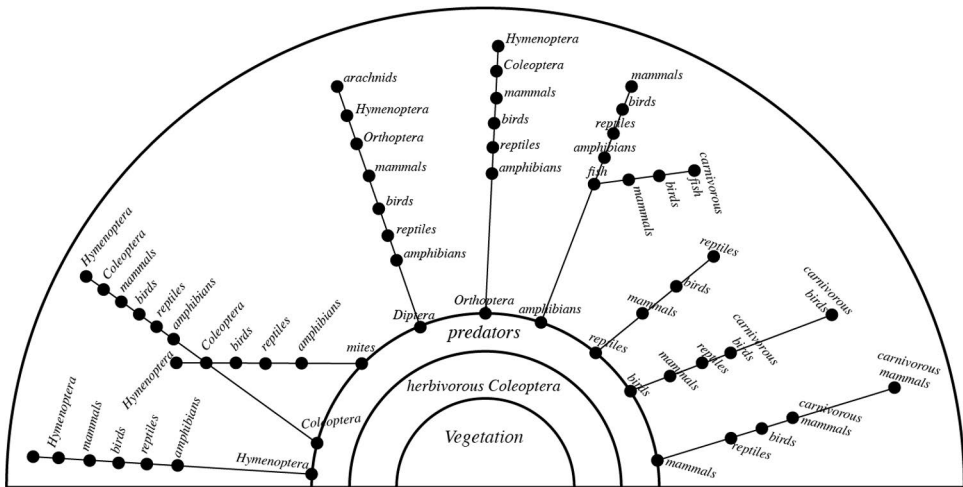
Species are tied through intimate relationships—species interactions—that they build with other species. Among possible relationships (e.g. predation, competition, amensalism, mutualism, and commensalism, Morin 2011), trophic

interactions help maintain the balance in nature by keeping species populations healthy, and by limiting the growth of populations, for example through extraction of part of the resource (e.g. predation or herbivory, Lotka-Volterra predator-prey model, Gotelli 2001). Trophic relationships form the backbone of ecosystems by channeling the energy from resources to consumers, forming the food web. Food webs are networks that describe the ‘who eats whom’ of ecosystems through interactions of species as links and nodes of the network; and the ‘by how much’ through quantitative information associated with the nodes or links of the network (respectively, species abundance or biomass, and interaction strength or energy flux). Changes in the ‘who eats whom’ may lead to drastic changes in the structure of food webs that could lead to disruption throughout the network (trophic cascades, Curtsdotter et al. 2011). The recent environmental and human-induced threats are forcing a restructuring of ecosystems worldwide: additions and losses of trophic interactions through the invasion of new species, and the local extinction of others, or shifts in the diet of recipient species. If we hope to better manage and protect ecosystems, we need to recognize that species are part of a giant, globally connected network that is ever changing (Poisot et al. 2015, Albouy et al. 2019). Our ability and efficacy at understanding how food webs have changed in the past will determine our ability to anticipate future ecosystem change.

The representation of species and trophic interactions as a web has a long history. In fact, already in 1859, Darwin pointed out that “... *plants and animals, most remote in scale of nature are bound together by a web of complex relations*”. A few decades later, Camerano (1880) provided the first graphical representation of a network of ‘enemies’ (Fig. 1). The early representations were already complex objects with the sole purpose of providing a graphical summary of interspecific interactions. However, it was not until 1927 that food webs became a distinct entity in ecology, when Elton (1927) theorised the concept of food chains and connected food chains, or ‘food cycles’ (later known as food webs). He observed that if animal communities organized around feeding hierarchies such as food chains and food webs, there must be a set of rules that govern the structure of food webs. Elton observed (i) the role of body size, and that on average consumers must feed within a limited range of prey sizes; (ii) that taxa occupy a niche corresponding to their role in the community, roles that could be filled by any other taxa occupying the same niche; (iii) that organism abundances decrease towards the top of the food chain; and finally, (iv) that the effect of species can propagate through the web. This pioneering work set the foundations for development of the food web concept (Layman et al. 2015). Since the work of Elton, development in the field of food web ecology split between three major fields: topological food webs (a.k.a. connectedness webs), energy flow food webs, and functional food webs (Layman et al. 2015). Food web topologies focus on understanding the architecture of ecosystems, so-called ‘food web structure’, and



use a set of tools derived from network theory to determine how food webs are structured (May 1972, Cohen et al. 1990, Delmas et al. 2019). Topologies are often static but because they can be represented as a binary matrix of interactions, they are ideal to map an overview of ecological communities. Flow food webs, on the other hand, describe trophic dynamics and focus on how energy flows from resources to consumers: trophic dynamics help us understand how nutrients and organic matter circulate within an ecosystem (Lindeman 1942). Last, functional food webs describe how the biomass of predators may unequally control the biomass of prey populations, and that some consumers exert a stronger control on some of their prey (Paine 1980).



**Figure 1.** Simplified reproduction of one of the first food webs reported in the literature (Camerano, 1880). The food web originally included more links (e.g. parasites), which were here removed for readability.

### 1.1.2. From structure to function

Our ability to understand how ecosystems change over time is tied to our understanding of how food web structure is changing. The reason is simple: the structure of any system will affect its function (Strogatz 2001). In the case of ecosystems, the organisation of species and trophic relationships that govern the structure will influence the functioning of ecosystems (Yen et al. 2016). Thus, the topology of food webs controls how information (like energy or perturbations) flows through the system, and ultimately can influence ecosystem functions such as productivity or stability (Duffy et al. 2007, Rooney and McCann 2012). That is because there is a reciprocal relationship between biodiversity (species composition and richness), productivity, and stability of ecological communities (Worm and Duffy 2003), and that food webs are the cement that binds these components together (Thompson et al. 2012). In fact, ecosystem functions often intertwine as the species populations supporting those functions are regulated by

trophic interactions (Duffy 2002). Because species are linked through trophic interactions, changes in the dynamics of species, or the complete loss of certain taxa, can lead to drastic alteration of ecosystems. For instance, the collapse of the *Gadus morhua* population in the Baltic Sea released its prey from predation and led to a trophic cascade causing the proliferation of filamentous algae (Reusch et al. 2018). Trying to link biodiversity to ecosystem functioning without incorporating food webs is like forgetting that species are never alone. It equals to forgetting one of the two components of biodiversity (Hines et al. 2015): the horizontal diversity (i.e. the heterogeneity in species within trophic levels, for example the diversity in plants) or the vertical diversity (i.e. the diversity across trophic levels, for example plants, herbivores, and predators).

Whereas the importance of species diversity in maintaining ecosystem functions is accepted, how food web structure specifically influences ecosystem functioning is still unclear. One of the longest standing debates has been around how food web complexity influences ecosystem stability (Landi et al. 2018). Food web research first hypothesised that higher diversity begets greater stability because the energy could be distributed along more pathways (MacArthur 1955). The theory showed that in more diverse communities, species can specialise to avoid competition for resources and that predation pressure can be distributed across prey species to maintain both prey and predator populations. However, mathematical models of randomly assembled food webs revealed that more diverse communities did not lead to more stable communities (May 1972). The clashing results paved the way for more studies that used empirical food webs (Cohen et al. 1990). Studies have later shown that the structure of real food webs is not random but often difficult to reproduce: it requires at least some constraints on the size, complexity, and the proportions of predators and prey in the modelled food webs (Pimm 1980). That is because (i) species participate in various essential topological substructures called 'motifs' (Milo et al. 2002, Stouffer 2010), (ii) not all interactions are equal in strength, and the balance of both strong and weak interactions is essential (Paine 1966, Wootton and Stouffer 2016), and (iii) some species have a disproportionate influence, irrespective of their biomass, on the food web structure and dynamics by the nature and strength of interactions they are involved in (i.e. 'keystone species', Paine 1966, 1969). Studies on prehistoric food webs have shown that ecological communities assemble along topological patterns that have evolved and persisted through time to lead to mature communities (Dunne et al. 2008). With certain structures, ecosystems can withstand the test of time. For instance, the complexity of food webs, and how trophic links are distributed among species, was found to influence the robustness of ecosystems to perturbations such as loss of biodiversity (Dunne et al. 2002, Dunne et al. 2004).

## 1.2. Studying temporal variability in food webs

Despite the greatest efforts, observing food webs over time (or space) is challenging. The reason is simple: food webs are complex and dynamic, and the components at their core (species and their trophic interactions) can vary in intricate ways laborious to observe, let alone to disentangle. Studies using low-complexity food webs have shown that food web structure may vary from an instant to another, from season to season, from year to year (Schoenly and Cohen 1991, Tavares-Cromar and Williams 1996). Compiling a single food web already represents a great feat as one needs to record all species and trophic interactions in a defined area. Increasing the temporal resolution, while accounting for all species and trophic interactions makes the task more speculative than real if we cannot record an instant snapshot of the food web. Consequently, few have studied temporal changes in the structure and function of food webs (but see, e.g., Table 1 in Schoenly and Cohen 1991), and either lacked in temporal resolution (e.g. consisting of a few temporal snapshots of a topology, typically a before-after state, Kaartinen and Roslin 2012, Yletyinen et al. 2016, Bodini et al. 2017), or focused their efforts on the dynamics of a few species of interest (Skaret and Pitcher 2016). Additionally, it is often unclear what drives changes in food web structure, as the species composition, the trophic links, or both, may vary.

Part of food web temporal variation can be observed, measured, or estimated (e.g. which species are there, and in which quantities). The community composition of the food web may vary in two ways that will influence food web structure: through species presence/absences, and species relative abundances. Changes in species presence/absence can be observed via species inventories. For instance, species composition may vary as a result from local species invasions or local extinctions (Pimm et al. 2014, Ojaveer et al. 2017). Immigrating species, as well as species in the recipient communities, will find new feeding opportunities (e.g. Kortsch et al. 2015, Herlevi et al. 2018). As species composition changes over time, new trophic links are added to the food web as species fall prey to predators, or become predators in the recipient communities. Trophic links are removed as species involved in those interactions go locally extinct (Thierry et al. 2011, Bartley et al. 2019). Knowing or estimating what the species composition is going to look like from one time step to the next, we can identify possible trophic interactions that originate from changes in species composition on the assumption that similar species most likely engage in similar trophic interactions. For instance, it is likely that consumers target a resource morphology matching their own traits, morphological requirements that transpire through the taxonomies of similar interacting species (Cattin et al. 2004). Species composition may also stay constant but trophic links could appear and disappear with shifting species abundances: the higher the abundances of pairs of species, the more likely they will meet by chance (i.e. neutral processes, Hubbell 2011). Last, trophic links may vary in how much energy travels through them. Fluxes of energy can be estimated from what we

know of the biology of each species and their metabolism (Barnes et al. 2018). How energy travels throughout the food web informs us about the functioning of the ecosystem.

Another part of food web temporal variation relates to the mechanisms behind species occurrence and trophic interactions (e.g. why they are where they are, and why they interact) and is challenging to understand and evaluate since it requires a broad understanding of community assembly rules, and ecosystems as a whole (Diamond 1975). The occurrence of species and trophic interactions may also have more subtle mechanisms that will determine the rewiring of food webs, and pertain to conditions at the interplay between local abiotic and biotic environments (Bartley et al. 2019). This information is much more difficult to collect, and will depend on how organisms sense and respond to their environment. Organisms sense and respond to their environment through a set of functional traits. Functional traits are defined as any morphological, physiological, phenological, or behavioral characteristics measurable at the individual level, and that impact fitness (as defined in Violle et al. 2007). Among them, response traits are a set of characteristics that influence individual responses to the environment (Díaz et al. 2013). Which response trait a species is equipped with, together with trade-offs in how they are expressed, determines species coexistence, shapes ecological communities, and can be seen as the phenotypic expression of ecological niches (Litchman et al. 2007). For instance, functional traits are the expression of physiological tolerance and requirements along the niche axis, and can explain species affinities for certain environments (Cadotte and Tucker 2017). They determine where offspring of species will go (dispersal filtering), and where they will successfully settle (environmental filtering). Finally, they will determine the viability of their coexistence with other species, and thus, if they will be suppressed by local competitors and predators (interaction filtering), making co-occurrence of species hardly synonymous with realized trophic interactions (Blanchet et al. 2020). For instance, competing species will tend to use habitats differently to reduce competition for a resource which could influence interactions with other species (i.e. niche partitioning, Finke and Snyder 2008). Therefore, direct and indirect interactions can reshape communities in unexpected ways, and even negate co-occurrence, which makes evaluation of possible trophic interactions difficult for complex communities (Cazelles et al. 2016). Last, although two species could meet in space and time, there is no guarantee for interactions to happen between them. Functional traits may act as locks and keys, where matching of the correct traits of the consumer and resource can enable trophic interactions (i.e. trait matching, Bartomeus et al. 2016). Variability in traits throughout the life of a species could, thereby, determine changes in their diet.

### 1.3. From descriptive metawebs to dynamic food webs

To study temporal variation in food webs—dynamics of structure and function—we need a framework that can integrate and expose multiple changes of biodiversity in the food webs. We need ways to reproduce the variability in structure and function (temporally resolved food webs that account for changes in species, trophic links, abundance and biomass), and tools to capture that variability (food web metrics). As of today, food web topologies focus solely on the skeleton of food webs and map static representations of trophic interactions (e.g. Barents Sea food web, Planque et al. 2014). Topologies tend to give comprehensive overviews of ecosystems as they only require an inventory of species and their trophic interactions, with no quantification whatsoever of the diet preferences of species, consumption rates, or energy transfer efficiencies. Metawebs are large cumulative topologies that account for all species, and integrate all possible interactions across spatial and temporal scales. This disregards spatial and temporal variability in environmental conditions and biotic interactions that shape ecological communities (Diamond 1975, Cadotte and Tucker 2017). Because of their data-aggregation nature, cumulative food webs have often been criticized to alter reality compared to empirical food webs collected *in situ* (Dunne 2006). Alone, cumulative food webs can seem limited. However, cumulative food webs have the advantage that they can be built from published literature or databases on diet of consumers (e.g. GloBI, Poelen et al. 2014; or DAPSTOM, Pinnegar 2014), compared to costly comprehensive ecosystem surveys. Thus, they can serve as a raw depiction of the food web from which we can extract temporally resolved food web snapshots.

A diverse set of metrics, including both qualitative and quantitative descriptors, is likely needed to analyse food web temporal variability. Food web descriptors need elements in their mathematical description able to detect variation in species composition, in species quantities (abundance, biomass), trophic link realization, and/or flows. Topological food webs (which most temporally-resolved studies have relied on) are usually described by a set of qualitative descriptors. Qualitative analyses focus on capturing patterns in the distribution of species and links, where species and links are considered equal and given the same weight. Consequently, qualitative descriptors cannot reveal changes when they originate from variations in the species quantities or trophic links that do not lead to the addition of new species or new links, or the complete removal of species and their links. Quantitative descriptors, on the other hand, were designed to incorporate differences in magnitude that are represented inside dynamic food web models (Bersier et al. 2002). Available quantitative descriptors have often ascribed information to the links in the food webs (e.g. transfer of energy). Dynamic food web models assume mass-balance—the energy entering the ecosystem equals the energy leaving the ecosystem—that is often problematic to estimate and

parameterize at the scale of an ecosystem. The heavy computational demand often limits the complexity of food web models that we can use, and make such descriptors unfit for studying food webs with more than a few dozen trophospecies (i.e. groups of taxa sharing similar attributes): two dynamical models of the Barents Sea by Dommasnes et al. (2001) and Skaret and Pitcher (2016), respectively contain 30 and 58 trophospecies, compared to 244 for the Barents Sea comprehensive topology (Planque et al. 2014). Requirements for high temporal resolution further limits the use of such descriptors as fluxes will need to be re-evaluated for each time step. For high-resolution food webs (where nodes are represented by species, rather than less resolved taxa), a trade-off between complexity and temporal resolution will typically be needed to use dynamical models and quantitative descriptors. Such trade-offs will often require simplification of the underlying topology, which is known to alter the structure of the food web (Pinnegar et al. 2005), as discussed later in this introduction. Other information that can serve as a proxy for the dynamics described by energy transfer will be needed for complex food webs. I propose the use of descriptors that incorporate quantities of species (abundance or biomass), as the ultimate outcome of influxes of energy and outfluxes of energy is the production or extraction of individuals from populations. Moreover, descriptors that incorporate quantities of species may also identify temporal variability when the topological distribution of species and their links remains unchanged.

## **1.4. Methodological challenges to building, using, and studying dynamics in complex food webs**

### **1.4.1. Temporal data scarcity and the simplification of food webs**

Before we can build temporally resolved food webs, one crucial step, often neglected when building food webs, is to assess the resolution of food webs. Uneven food webs arise when data is scarce, either on the description of species, of their links, or both. When looking at temporal food web snapshots, it may result in some species being disconnected from the food web because we could not record observations of species they interact with and their links. It raises one important question: what to do when data on how an organism interacts is lacking? Food webs are usually biased vertically towards predators and organisms at the top of food chains because (i) diversity is much larger at the bottom of the food web where organisms are small and often unicellular, (ii) we usually report trophic interactions from the perspective of the consumer (gut content analysis, *in situ* feeding observations), (iii) larger organisms are often easier to sample, more commercially interesting, and thus more studied. Food web resolution can also be biased horizontally within trophic levels where dominant and persistent species are more frequently reported, whereas rarer and less frequent species are often poorly described. When trophic information is lacking, one solution could be to

either ignore a taxon all together, including its known trophic interactions (in- and out-going links), or to infer possible interactions based on similarity with other species (e.g. taxonomic relatedness, Cattin et al. 2004, or trophic similarity, Sugihara 1989). However, removing a taxon may propagate the scarcity of information to other taxa that then need to be re-evaluated, and adding more uncertain links will likely pathologically inflate the number of links and lead to a wrong estimation of food web properties (Dunne 2006, Jordán and Osváth 2009). Another solution is to group that species with others that may have a similar role in the food web so as to limit duplicates of links that may not exist.

The process of grouping species—also known as **food web aggregation**—is often unavoidable. Aggregation of species and their links can provide several advantages if used carefully: to even resolution across trophic levels, to complete information when data is lacking, or to reduce the size of food webs for computational purposes. Aggregation has often been used to simplify food web topologies for Ecopath models (e.g. Dommasnes et al. 2001, Mackinson and Daskalov 2007). However, several isolated studies have raised concerns on how aggregation methodologies and the choices we make (e.g. how to group species, how to group links) can alter the structure of the resulting food webs (Martinez 1991, 1993, Solow and Beet 1998, Pinnegar et al. 2005, Jordán and Osváth 2009, Jordán et al. 2018). Aggregation procedures are plentiful, and can combine various ways to aggregate species (e.g. based on taxonomic relatedness, Cattin et al. 2004, or trophic similarity, Martinez 1991), or aggregate their links (Martinez 1993). We have limited knowledge on how food web structural properties respond to combinations of varied aggregation methodologies. Still, most food web dynamical models aggregate larger counterparts to such extremes that they may be studying topologies distant from that of the real food web. Studies on the combined effect of species and link aggregation are needed if we want to ensure comparability across studies.

#### **1.4.2. The context-dependency of trophic links**

As detailed above, part of temporal variation in food web structure originates from changes in how trophic links are realized (over space or time). To date, we do not have a clear understanding of how the interplay of dispersal, environmental, and interaction filtering, as well as trait matching determines the spatiotemporal occurrence of both species and their trophic interactions. However, we know that functional traits influence the outcome, and whether new links will be added to food webs, and existing ones removed (i.e. food web rewiring). Functional traits not only influence the spatiotemporal occurrence of predators and prey, but in a context-dependent way enable, disable, magnify, or hamper trophic interactions through an evolutionary-ecological game in which predators and prey disarm each other's attacks and defenses. A deeper understanding of which and how consumer-resource traits enable and disable

trophic interactions is needed if we want to model the variability in trophic links expression, and incorporate rewiring of food webs in spatiotemporal studies.

Phenomenologically, functional traits have been shown to participate in structuring food webs, and even limited sets of traits suffice to reproduce the structure of food webs (e.g. body size, Eklöf et al. 2013, Laigle et al. 2018, Brose et al. 2019). For instance, body size was identified as the number one trait that governs the food web structure (Brose et al. 2006). Functional traits are also central to organism responses to variability in their environment, and can determine the timing of species co-occurrence, and subsequently, the potential for and timing of trophic interactions. If we can elucidate the mechanisms behind the occurrence of trophic interactions, we might be able to better understand which species interactions are likely to be realized, in different abiotic and biotic contexts. Topologically, functional traits enable or disable trophic interactions through a set of lock-and-key rules, where matching of the correct consumer-resource traits is needed for interactions to occur (i.e. trait matching, Bartomeus et al. 2016, Gravel et al. 2016). For instance, diel vertical migration strategies can be related to the length, sensory mode, and feeding mode species are equipped with (Pinti et al. 2019). In mutualistic networks (e.g. fruit-bird networks), strong consumer-resource relationships can be found across scales (Dehling et al. 2014). There are thereby likely sets of consumer-resource traits that enable or disable interactions in different ecological contexts, such as habitats. If we can identify such trait-matching rules, we may be able to profile or characterise interacting species, allowing us to bypass limitations in data availability (e.g. on trophic interactions) for food web compilation. Once we have identified such rules, biological traits present several advantages: sampling of resources and consumers no longer need to be simultaneous, nor time-bound; they describe the context in which species can co-occur in space and time, and interact; such information can be extrapolated to other species with similar trait values. Consumer-resource trait-based profiling could help build more realistic, and context-dependent food webs. For instance, consumer-resource profiles could help aggregate food webs into meaningful groups based on trait-matching rules, or help infer trophic interactions. If we can elucidate the mechanisms behind the occurrence of trophic interactions, we should be able to predict which species interactions will most likely be realized.



## 2. MAIN QUESTIONS ASKED IN THE THESIS

### 2.1. Aims and scope of the thesis

The overall aim of this thesis is two-fold. The first aim is to explore the temporal variability in food web structure and function. I aim to elucidate how temporal variation in food webs originates from changes in species composition, abundance, and energy fluxes. Second, I aim to find new ways to improve the building, use, and applicability of food webs. I consequently investigate long-term challenges in the building of food web topologies and provide guidelines on how we can improve transparency, reproducibility and comparability of food web studies. Overall, throughout my research, I want to impress upon the readers the cruciality of adopting multi-trophic approaches that integrate and leverage information derived from food webs.

My thesis consists of four papers. **Paper I** sets the foundations of my work exploring temporal changes in food web topologies by combining classic ecological network analysis of topologies with abundance data. **Paper II** expands on the findings and methodology of **Paper I** exploring temporal variation in food web structure and function, by also assessing temporal variation in energy fluxes. Temporal analysis of food webs has either relied on a limited before-after approach (e.g. before and after a regime shift, Yletyinen et al. 2016) or used simple, far-from-complete *ad hoc* food webs to investigate scenarios (e.g. the Ecopath with Ecosim approach, Christensen and Pauly 1992). Both approaches have their strengths and limitations, and my thesis aims at finding an approach at the nexus between both worlds. In **Papers I** and **II**, I strive for high food web temporal resolution and combine time series of species dominance (abundance, in **Paper I**, or biomass, in **Paper II**) with food web topologies. **Paper III** deals with a long-standing issue in food web science: aggregation of species and trophic links when data is lacking, resolution is uneven, or less complex food webs are needed for computational purposes. I use existing food web topologies to explore efficiency of aggregation procedures. **Paper IV** goes beyond species taxonomy and explores how morphological and behavioral characteristics of species tie consumers and resources together through matching of their respective biological traits. We will probably never be able to observe all possible trophic interactions at any given point in time or space, but identifying rules through which consumer and resource traits interact can help us assess which trophic interactions to include in food webs. **Paper IV** aims at identifying profiles of interacting consumers and resources, to in the future use that information for refining existing food webs or help identify novel possible trophic interactions.

## 2.2. Specific questions addressed in each chapter

### Paper I: German Bight

*In Paper I, I explore the temporal variability of a food web for the German Bight (North Sea), comparing unweighted (species composition) and weighted (species abundances) metrics describing topological structure.*

- I. Has the food web structure changed over time and how?
- II. Are the potential changes in the structure related to composition or relative abundances of taxa?

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### Paper II: Gulf of Riga

*In Paper II, I develop and combine a set of qualitative and quantitative descriptors (unweighted, node-weighted, and link-weighted metrics) to investigate the temporal relationship between food web structure and function in the Gulf of Riga food web (Baltic Sea).*

- I. How does food web structure and function vary over time?
- II. Do unweighted and weighted metrics highlight different (or similar) aspects of temporal food web dynamics?
- III. Can we identify trends in the structure and function of the Gulf of Riga community?

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### Paper III: Barents Sea

*In Paper III, I use the Barents Sea food web to explore the performance of aggregation methods at maintaining food web structure, and to assess how food web structural properties vary with methodologies and levels of aggregation.*

- I. Which structural properties are sensitive (or insensitive) to aggregation procedures?
  - II. Are there methodologies that perform better at maintaining food web structure?
-

#### **Paper IV: Åland Islands**

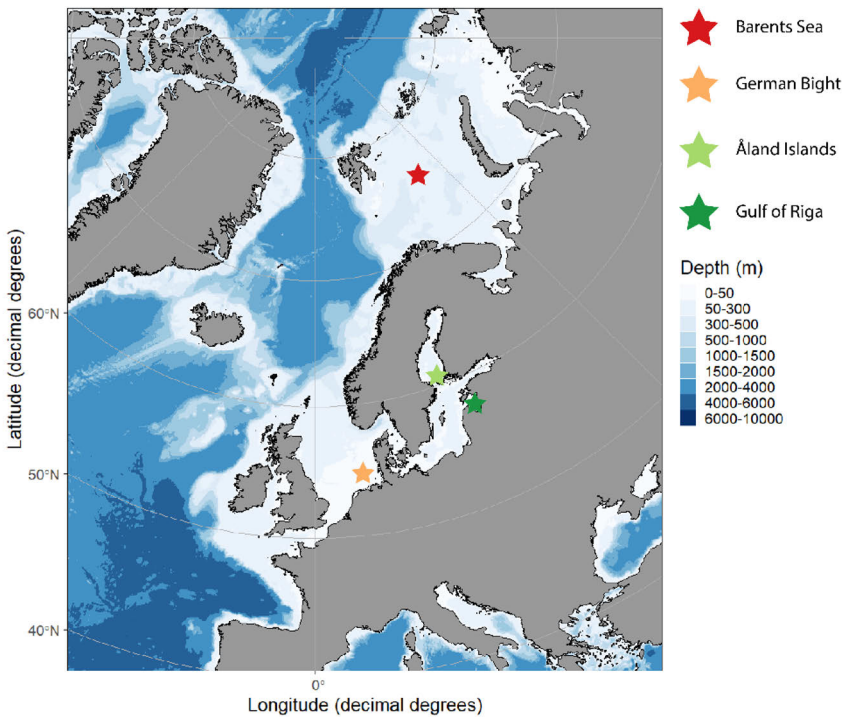
*In Paper IV, I go beyond species taxonomy to investigate which and how consumer and resource traits participate in structuring the food web. I build a trophic-link based trait-interaction network—or trait web—to explore associations between consumer and resource traits across habitats in the Åland Islands (Baltic Sea).*

- I. How are communities and food webs structured at the local scale?
- II. Which traits contribute to the observed food web structures?
- III. How are consumer-resource trait associations structured? Are there groups of more strongly interacting traits?

### 3. MATERIAL AND METHODS

#### 3.1. Case studies and study regions

In this work, I use food webs from several regions (Fig. 2) for the availability of data and the complexity of the food webs they harbor. I relied on food webs compiled by others as well as compiled my own food webs to meet the needs of specific studies. The specificities of each region and associated food webs are described in the following sections, as well as in Table 1 and Table 2 (respectively).



**Figure 2.** Bathymetric map showing the overview of the study sites for which each food web was compiled. The Barents Sea food web represents a basin-scale food web, whereas other food webs are local.

##### 3.1.1. The North Sea

The North Sea is a well-studied shallow shelf sea characterized by water masses covering a broad range of salinities from high salinity waters (35 PSU) brought by the Atlantic Ocean in the South and in the North, to low salinity waters (27 PSU) in estuaries and coastal waters with input by rivers. Extreme changes in salinities occur more at the coast with large freshwater runoffs in the spring that dissipate

and mix with more saline Atlantic waters in the Central North Sea (Ehrich et al. 2007). The salinity drops towards the East as the North Sea exchanges waters with the Baltic Sea (lower salinities) via Skagerrak. Sea surface temperatures vary with great amplitudes from sea ice formation in winter and temperatures sometimes reaching over 20°C in summer. The hydrography and differences in temperature, especially, influence the biodiversity in the North Sea and segment the North Sea into subregions boarded by water fronts separating thermally stratified and mixed areas (Narayanaswamy et al. 2010). The distribution of species changes inter-annually and seems most influenced by the severity of winters that impact macrofaunal communities most sensitive to changes in sea bottom temperatures (Kröncke et al. 2011, 2013).

The few food webs available for the North Sea are often regional and built for use in ecosystem models, limiting how much information is available for comprehensive analyses of food web topology. However, the long practice of reporting changes in biodiversity, and repeated fine-scale ecosystem surveys (e.g., GSBTS, Ehrich et al. 2007), makes the North Sea an ideal region for building a temporally resolved food web.

**Table 1.** Comparison of the oceanography of the regional seas studied in the four chapters. The oceanographic data was extracted from Ozhigin et al. (2011) and Kortsch et al. (2019) for the Barents Sea, Otto et al. (1990) and Huthnance (1991) for the North Sea, and Snoeijjs-Leijonmalm et al. (2017) for the Baltic Sea.

Regional Seas	Mean Depth	Temperature (Mean SST)	Salinity (SSS)	Climate	Study
Barents Sea	230m	-1.5 – >7.5°C (August mean)	31.0 – >35.0 PSU	Subarctic- Arctic	Paper III
North Sea	80m	<13 – >18°C (August mean)	27 – >35 PSU	Temperate	Paper I
Baltic Sea	57m	14 – >20°C (August mean)	<2 – >30 PSU	Subarctic- temperate	Paper IV Paper II

### 3.1.2. The Baltic Sea

The Baltic Sea is a young semi-enclosed shallow nontidal brackish-water shelf sea with a unique hydrological and ecological system (Ojaveer et al. 2010, Reusch et al. 2018). The Baltic Sea stretches over more than 1,400 km and encompasses a temperate climate in the south, and a boreal climate with sea ice coverage in winter in the north. The frequency of saline water inputs from the North Sea and regularity of riverine inflows to the Baltic Sea control the salinity in the Baltic Sea. The strong difference in density between saline bottom water from the North Sea and surface freshwater from the Baltic Sea creates a ~2,000 km large and strong spatial salinity gradient decreasing from Skagerrak (southwest) to the Bothnian

Bay (northeast) that controls diversity patterns in the Baltic Sea. Diversity is generally low with taxonomic diversity decreasing from the south to the north. The southern regions are more largely dominated by marine species whereas the northern regions are more largely dominated by freshwater species (Ojaveer et al. 2010). Diversity has remained low as the strong differences in salinity creates a stressful environment that limits the establishment of viable populations for invasive species. The low diversity in the Baltic Sea makes this area ideal to study processes that require detailed food web topologies. However, to this day, few studies have used high-resolution food webs. We have compiled two detailed food webs, one for the Åland Islands and one for the Gulf of Riga.

**Table 2.** Description of the local food webs included in the four chapters. The food webs either describe the entire sea or a specific location.

Regional Seas	Food web	Food web type	Functional groups	S	L	Z	C	Source
Barents Sea	Barents Sea	Benthopelagic	Phytoplankton, zooplankton, invertebrates, fish, seabirds, marine mammals	233	2218	9.52	0.04	Planque et al., 2014
North Sea	German Bight	Benthic	Phytoplankton, zooplankton, invertebrates, fish	55	588	10.7	0.19	Paper I
Baltic Sea	Archipelago Sea	Benthic	Phytoplankton, zooplankton, benthic invertebrates, fish	61	452	7.41	0.12	Paper IV
	Gulf of Riga	Benthopelagic	Phytoplankton, zooplankton, benthic invertebrates, fish	34	207	6.09	0.79	Paper II

### 3.1.3. The Barents Sea

The Barents Sea is a large shallow marginal shelf sea located in the Arctic Ocean. It is composed of regions distinct in their topography, hydrography and species distribution: the boreal region, the polar front and the Arctic region. The boreal region is influenced by warm and highly saline Atlantic waters. The Arctic region under the influence of seasonal sea ice coverage is governed by colder waters. Finally, the polar front at the interface between the two former regions marks a transition zone for warm salty waters moving north from the Atlantic Ocean and cold fresher waters moving south from the Arctic (Loeng and Drinkwater 2007). Additionally, the Barents Sea food web is here unique in that it combines marine and terrestrial components with terrestrial predators as the polar bear (*Ursus maritimus*) uses the sea ice to hunt on marine mammals (e.g. the bearded seal, *Erignathus barbatus*, Andersen and Aars 2016). In the Arctic region, the marine realm also depends to a large extent on the sea ice from the sedimentation of decaying sea ice diatoms that fuels the marine benthos.

Studying food webs in the Barents Sea has a long history (Bear Island food web by Summerhayes and Elton 1923) and several food webs of increasing complexity

and comprehensiveness can be found in the literature, often built for the purpose of studying a specific functional group or compartment of the environment (e.g. Ciannelli et al. 2005, with a focus on fish; Arndt et al. 2009, with a focus on sea ice; Gabrielsen 2009, with a focus on seabirds; Vadstein 2009, with a focus on plankton). Other food webs were built to give a comprehensive overview of the Barents Sea ecosystem but with different levels of resolution for the taxa included (e.g. Dommasnes et al. 2001, Bodini et al. 2009, Planque et al. 2014). The availability of numerous food webs built for diverse purposes made the Barents Sea food web ideal for investigating our efficiency and accuracy in reproducing and deriving patterns in food web structure, especially when aggregating food webs to less resolved counterparts (**Paper III**).

## 3.2. Compilation and selection of data

Compiling food web topologies with the aim of studying food web structure and function requires knowledge on which species are present, what they eat, and what they do. The first two types of information are essential to build food web topologies, whereas knowing what species do can help refine existing information or allow inference of possible interactions between species when data is scarce or lacking.

### 3.2.1. Who they are: Species composition

For this thesis, I built or helped build several food webs from the ground up (e.g. German Bight, Åland Islands and Gulf of Riga food webs). Selection of species always started with an inventory of taxa that I acquired through *in situ* sampling (e.g. Åland food web) or through accessing existing ecosystem surveys (e.g. German Bight or Gulf of Riga food webs). Food webs in **Papers I**, and **II** relied on ecosystem surveys that assess the occurrence of species in the North Sea, and the Gulf of Riga in the Baltic Sea. Relying on fine-scale, annual sampling (such as in annual ecosystem surveys) as the basis for compiling food webs allows for a resolution that is needed for observing changes in food web structure and function over space and time. In my thesis, I focus on temporally resolved data. In **Paper I**, I relied on the German Small-scale Bottom Trawl Survey (GSBTS), which has collected benthic epifauna and demersal fish in several selected areas across the North Sea, annually in summer since 1998 (Ehrich et al. 2007). I focus on the sampling area located in the German Bight. The fish community was sampled with an otter trawl, whereas benthic epifauna was sampled with a two-beam trawl. In **Paper II**, we used long-term biomonitoring data for phytoplankton, zooplankton, benthos, and fish, sampled over 38 years from 1979 till 2016. We focused on spring/early summer data to respect seasonality and habitat dependencies across taxa. To select species for the analyses in **Paper I** and **II**, I chose two criteria: abundance or biomass levels to select the majority of the species community, and temporal persistence to include recurring species. Persistence was determined by

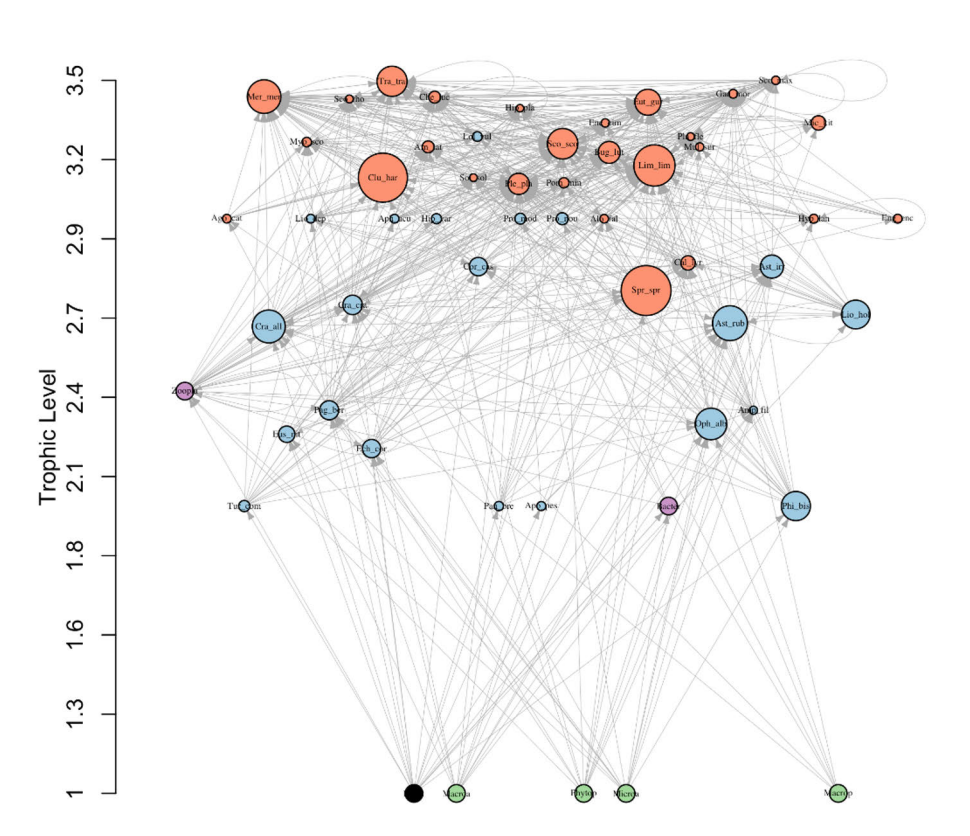
fitting a third-order polynomial between the log of abundance and number of years of presence (following Genner et al. 2004). The point of inflection in the curve indicates the minimum number of years for species to be considered temporally persistent. In **Paper III**, I used the pre-existing Barents Sea food web as the basis for my analysis. The food web was originally assembled using multiple sources on species distribution data (Planque et al. 2014). Finally, in **Paper IV**, I sampled the benthic communities in four different habitats for an overview of the species assemblages associated with these common coastal habitats (*Fucus*, *Zostera*, sandy substrate and rocky substrate). In addition to the recorded taxa, we completed the food webs with functional groups essential for the functioning of food webs, but that were not sampled in the surveys (e.g. detritus, zooplankton, phytoplankton in the German Bight food web).

### 3.2.2. What they eat: Trophic interactions

Documentation of feeding links among marine taxa can e.g. be done through (i) gut content analysis of the consumers, (ii) *in situ* observations by diving or filming, and (iii) feeding experiments *in situ* or in the lab. Ideally, it is preferable to collect information on all trophic interactions simultaneously with the species inventory to ensure obtaining a food web as representative of the actual food web as possible, without influences from temporal variability in trophic link expression. In practice, complete simultaneous sampling is hardly possible, and we are only able to depict snapshots of the real food web, snapshots that may well only hold true at the actual time the trophic interactions were observed.

The food webs used in my thesis represent **metawebs**, i.e., master food webs including all reported species and their trophic interactions (for instance, the German Bight metaweb from **Paper I**; Fig. 3) from which one can subset more spatially and temporally detailed food web snapshots. For these metawebs, I collated information on trophic links through stomach content analysis, extensive literature reviews, and accessing existing databases on trophic interactions or stomach content analysis (e.g. GloBI, Poelen et al. 2014, DAPSTOM, Pinnegar 2014). When collecting diet data from the literature, I used scientific literature search engines (e.g. Google Scholar, Web of Science) and digital collections of scientific reports. I built my search queries to include synonyms of species names as species names regularly change in the literature. I referenced each record of a trophic interaction (e.g. data on individuals such as size, life stage) together with the location of the observation, the method of observation, and justification for why a trophic link was included if inferred from observations of other species (e.g. with similar morphology, Cattin et al. 2004). Referencing each trophic interaction allowed me to evaluate the quality of the information included in each food web, helped me incorporate trophic relationships collected previously to build new food webs, as well as expand existing food webs. The method for evaluating data quality is described in **Paper I** Supplementary A2.





**Figure 3.** Metaweb of the German Bight. The y-axis indicates the trophic levels of the species. Arrows pointing upward represent trophic links, and connect resources to consumers starting from basal species at the bottom. The size of the nodes is proportional to quantities of species, here, the mean log-transformed abundance of species over the 18-year time series (see **Paper I**). Selected species are represented by their name abbreviations on the node (see species list). The color of the nodes indicates which functional group they belong to: red, blue, purple, green, and black nodes correspond to fish, invertebrates, grazers, primary producers, and detritus.

The food web data collected in **Papers I, II, and IV** were completed with a thorough literature review on diet of the species reported in the food webs. When diet information was lacking, I inferred trophic links based on the diet of, or feeding on, taxonomically related species following the assumption that taxa sharing similar characteristics (e.g. morphology) would target the same resources and be fed upon by similar consumers (Laigle et al. 2018). I also assumed that two co-occurring taxa were neutral to the context so that if they were previously observed to interact, they could interact at any given time and location. However, co-occurrence of taxa is not synonymous with realized interactions and some possible

trophic interactions may not be realized at all time (Cazelles et al. 2016, Freilich et al. 2018, Blanchet et al. 2020). The metawebs in this thesis thereby represent collections of possible trophic interactions for the studied food webs.

Finally, to evaluate completeness of the diet information, I used two complementary methods. First, I used species accumulation curves to evaluate completeness of field sampling. The method originally calculates accumulation curves from samples, reaching a plateau once no new species are added to the pool of species found in previous samples. Similarly, I sampled trophic interactions considering the literature references as samples, and estimated completeness of the literature review using the 'Chao' estimator as described in the supplementary of **Paper I** (Appendix 2, Olivier et al. 2019). For well-studied species (e.g. cod, herring, flounder), the data reached a plateau. For lesser-studied species (e.g. *Pandalina brevirostris*, *Turritella communis*, *Aporrhais pespelecani*), the literature available was limited, and it was impossible to get an accurate estimate on diet completeness using species accumulation curves. Instead, I calculated trophic positioning (trophic level) of the species in the studied food webs and compared it to values found in the literature (e.g. FishBase, Froese and Pauly 2021), or asked for an expert opinion. For the calculation, I wrote a sequential algorithm that built food webs from the bottom-up starting with trophic level 1 (basal species). Using this method, I could, for instance, identify misplaced predators that would inaccurately position low in the food web (e.g., trophic level 1 or 2). The combination of species accumulation curves and trophic positioning evaluations was powerful in identifying errors or gaps in available information. Species were removed from the food webs in the case where diet data was still insufficient, even after several rounds of literature review and diet completeness evaluation (e.g., species misplaced within the food web or disconnected from the network).

### **3.2.3. What they do: Biological traits**

Response and effect traits dictate how species respond to their environment (e.g. body size, egg size, elusiveness), and how they affect their environment and the species living with them (e.g. migratory status, food type, sediment transport capability, Díaz et al. 2013, Gravel et al. 2016). Describing which traits compose ecological communities can help understand why species are where they are, and whether they are able to interact (i.e. through trait matching, or the concept of so-called forbidden interactions, Morales-Castilla et al. 2015, Bartomeus et al. 2016). In **Paper IV**, I explored how traits of consumer and resource taxa interact through trophic interactions. I collected information on biological traits assumed to influence optimal foraging (i.e. benefit between the energy allocated to the search, capture, and consumption of a prey; and the energy gained from that prey). More specifically, I focused on topological traits that govern the ability of consumers to detect, capture and consume resources, and for a resource to avoid or defend itself against a consumer's attacks (e.g. consumer type, mobility of the

consumer compares to that of the prey, body mass, Gravel et al. 2016). Eklöf et al. (2013) identified that the traits body mass, metabolic category, feeding strategy, consumer type, and habitat, allow us to reproduce the structure of empirical food webs. I expanded this set to include body shape, protection, gut morphology, and mobility. Traits either described characteristics of resources, consumers, or both, depending on whether they decreased vulnerability to predators, or increased attacks on resources. The quantitative traits were measured in the lab on sampled organisms that served to compile the Åland Islands food web, and qualitative traits were determined from the literature or photographs of sampled organisms. All quantitative traits were converted to categories to accommodate the needs of the statistical analysis. Traits were measured on individuals representative of the community, but not on prey in the guts of predators. Additionally, in **Papers I, II and IV**, I used trait information to infer trophic interactions. When information on trophic interactions is not directly collectable, we need to infer possible trophic interactions from what we know about the species. One way is to infer trophic interactions from closely related taxa (i.e. taxonomic relatedness, Gray et al. 2015), assuming that the diet of taxonomically related taxa follows similar constraints (Cattin et al. 2004). Another way is to consider that species that share biological traits (e.g. morphological traits) also share interactors. Taxonomically related species and species with similar traits often evolved following similar biological requirements and environmental constraints that control their responses to the environment.

### **3.3. Food web structure and function**

#### **3.3.1. Network analysis and food web metrics**

In all papers, I used Ecological Network Analysis (ENA). ENA is a set of methods applied to the study of the structure and functioning of ecosystems (Borrett et al. 2018, Delmas et al. 2019). Structural analyses use metrics that expose patterns in the topology of food webs. Flow analyses use input-output analyses to summarize how energy travels through the food web. In my thesis, I use a selection of qualitative and quantitative metrics from structural and flow analyses to provide an in-depth description of food web structure and function. A selection of the unweighted metrics, with their node-weighted and link-weighted equivalents, are described in Table 3. For a definition and mathematical formulas of each metric, see Table 1 of **Paper I**, and the supplementary S6 of **Paper II**. Qualitative, or unweighted metrics rely on binary data that represent the presence of species and the interactions between consumers and resources. I selected complementary and widely used metrics, such as the species richness of the food web ( $S$ , the number of taxa), link density ( $Z$ , the average number of trophic link per taxa), directed connectance ( $C$ , a measure of complexity out of all possible links), generality ( $G$ , a measure of the number of prey per predator), and vulnerability ( $V$ ,

a measure of the number of predator per prey). Qualitative metrics are relatively easy to compute and straightforward to interpret. Variability in qualitative metrics (as part of analyses of temporal changes in food web structure) relates to species and their links being added or removed from the food web. However, qualitative metrics consider all species and links to be equal when, in nature, that is not the case, as seen e.g. in differences in species abundances (Lyons et al. 2005) and interaction strengths (Paine 1966, 1980). Thus, I expanded my analyses with quantitative metrics that additionally reflect variation in species dominance (quantities, such as abundance or biomass), and in interaction strength (energy fluxes). In **Papers I** and **II**, I built food web topologies ascribing information to the nodes (i.e. abundance and biomass at a time step) on the assumption that the abundance or biomass of species at a time step is the output of population dynamics that occurred between time steps (i.e. the net sum of individuals that were eaten or emigrated, and individuals that were born or immigrated). This assumption allowed me to develop node-weighted metrics (e.g. wG, abundance or biomass-weighted mean of the number of prey per predators; and wV, abundance- or biomass-weighted mean of the number of predators per prey) to detect changes in the food web structure originating from changes in abundance and biomass, either weighting nodes by abundance (**Paper I**) or biomass (**Paper II**). The weight, thus, represents the ‘size’ of the population, and gives equal chance to each individual (in the case of abundance), to express the trophic links represented at the species level. The larger proportion of the community, the higher weight in the topology.

In **Paper II**, we additionally used link-weighted metrics, ascribing energy fluxes to the links of the Gulf of Riga food web. We assigned energy fluxes to the trophic links through a bioenergetic food web approach (Barnes et al. 2018, Gauzens et al. 2019). Quantifying energy fluxes allows us to assess species contributions to the functioning of ecosystems. The model relies on allometric scaling laws that quantify metabolic rates from individual body masses. The ecosystem survey in the Gulf of Riga collected, along with the species composition, species biomasses for most species that, multiplied by metabolic rates per unit biomass, allowed us to quantify metabolic demands for the species. We were able to estimate metabolic rates for fish, benthos, and phytoplankton, with the exception of zooplankton that were estimated using data from other regions of the Baltic Sea. From the metabolic demands, we are able to calculate in- and out-going fluxes to each species as the model assumes system equilibrium between the energy losses to predation and metabolism, and the energetic gains from consuming resources (i.e., the influxes multiplied by the assimilation efficiency to measure the actual portion of energy being assimilated, Barnes et al. 2018). The model follows a top-down approach so that losses to predation for top predators are assumed to equal to zero.

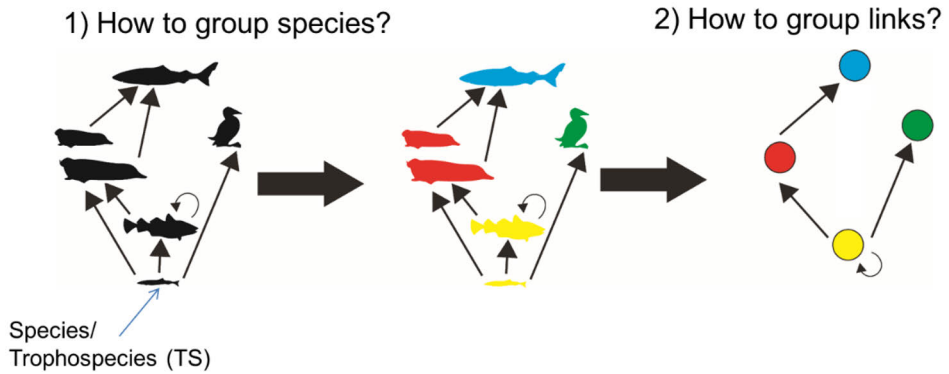
**Table 3.** Examples of unweighted metrics, with node-weighted and link-weighted equivalents. In the formulas,  $L$  denotes the number of trophic interactions in the food web,  $S$  the number of species or species richness of the food web,  $k$  represents any trophospecies,  $w_k$  is the abundance or biomass of trophospecies  $k$  (resource or consumer),  $a_{ik}$  is a prey  $i$  in the diet of predator  $k$ , (and conversely for  $a_{kj}$ ),  $n_i$  and  $n_j$  are the number of prey (or resources) and predators (or consumers) in the food web. In formulas,  $n_i$  and  $n_R$ , and  $n_j$  and  $n_C$  are equivalents.

Metrics	Definitions and formulas	Ecological implications	References
Linkage density (Z)	Average number of interactions per taxa $Z = \frac{L}{S}$	Informs on the repartition of trophic links among taxa in the food web	Dunne 2009
Directed connectance (C)	Proportion of all possible trophic links ( $S^2$ ) that are realized $C = \frac{L}{S^2}$	Relates to the complexity of the food web, and its robustness in the face of perturbations	Dunne 2009
Generality (G)	Mean number of prey per predator $G = \frac{\sum_{k=1}^j a_{ik}}{n_j}$	Indicates if the system contains more generalist or specialist species. In a more generalist system, more species are highly interlinked.	Schoener 1989
Node-weighted generality (nwG)	Abundance or biomass-based weighted mean of the number of prey per predator $nwG = \frac{\sum_{k=1}^j (w_k \sum_{i=1}^S (a_{ik}))}{\sum_{k=1}^j w_k}$	Indicates if the system contains more generalist or specialist species based on predator abundances	Paper I, II
Link-weighted generality (lwG)	Average effective number of prey taxa or resources over all consumer taxa weighted by in- and out-flows of a taxon $lwG = \sum_{k=1}^s \frac{b_{.k}}{b_{..}} * n_{R,k}$ <p>where <math>b_{.k}</math> represents the total amount of biomass coming to a taxon over <math>b_{..}</math> the total amount of biomass flowing in the system</p>	Considers the functional importance of a taxa as a consumer.	Bersier et al. 2002
Vulnerability (V)	Mean number of predators per prey $V = \frac{\sum_{k=1}^i a_{kj}}{n_i}$	Indicates the degree to which taxa function as prey and their vulnerability to predators	Schoener 1989
Node-weighted vulnerability (nwV)	Abundance or biomass-based weighted mean of the number of predators per prey $wV = \frac{\sum_{k=1}^i (w_k \sum_{j=1}^S (a_{kj}))}{\sum_{k=1}^i w_k}$	Indicates the degree to which taxa function as prey and their vulnerability to predators, based on their abundance or biomass	Paper I, II
Link-weighted vulnerability (lwV)	Average effective number of predator taxa or consumers over all resource taxa weighted by in- and out-flows of a taxon $lwV = \sum_{k=1}^s \frac{b_{k.}}{b_{..}} * n_{C,k}$ <p>where <math>b_{k.}</math> represents the total amount of biomass leaving a taxon over <math>b_{..}</math> the total amount of biomass flowing in the system</p>	Considers the functional importance of a taxa as a resource.	Bersier et al. 2002

### 3.3.2. Food web aggregation

Because we are unable to collect all trophic links for all species present in an ecosystem for a given point in time, food web scientists either often build food webs with uneven resolution (i.e. some species are partially represented), or include data from the literature that can be incorrect for local conditions, or outdated (i.e. temporal aggregation of data, Jordán and Osváth 2009). Typically, organisms at the bottom of the food web are less resolved because of their smaller size and larger diversity. Removing taxa when data is lacking should always be the last resort as consequences of the action may propagate through the network: it may remove links for other taxa that then need to be re-evaluated, and possibly removed as well. One solution is to aggregate similar species together to even resolution across trophic levels, to merge information when data is lacking, or to reduce the size of food webs for computational purposes. Aggregation is often used to simplify food web topologies for Ecopath models (e.g. Dommasnes et al. 2001, Mackinson and Daskalov 2007). However, used with the wrong methodologies, or pushed too far, aggregation can alter the structure of food webs (Pinnegar et al. 2005). The extent to which food webs are aggregated should never be arbitrary but follow careful examination of the behaviour of structural properties of the food web in question. In **Paper III**, I tested the sensitivity of food web structural properties to different aggregation protocols.

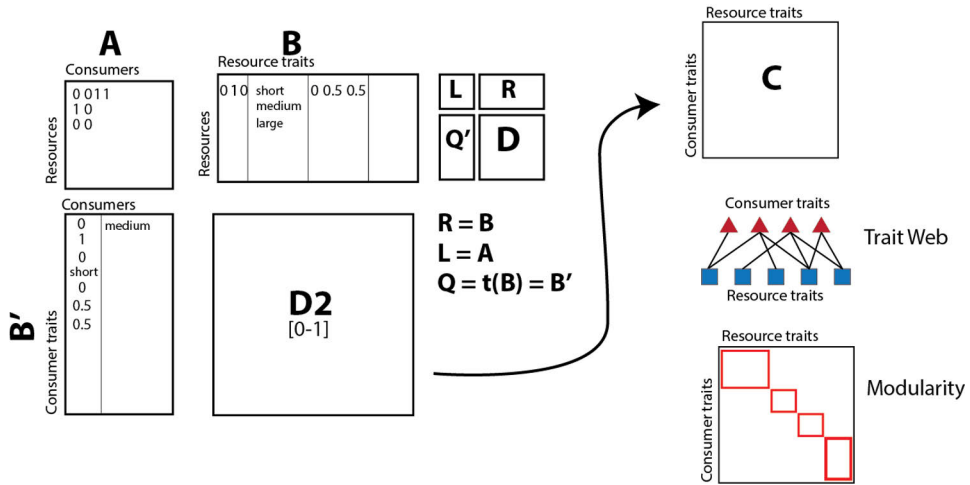
Aggregation procedures consist of two major steps: (i) identify which species to aggregate together into trophospecies (i.e. a group of species with similarities), (ii) decide how to aggregate their trophic links (Fig. 4). Aggregation of species can be performed in many ways. I selected three methods that describe different similarities between species: their taxonomic relatedness (taxonomic aggregation, Cattin et al. 2004), their role in the food web (regular equivalence aggregation, Borgatti and Everett 1993, Luczkovich et al. 2003), or their trophic similarity (structural equivalence aggregation, Martinez 1991, 1993). I then compared my results with food webs that were aggregated based on *ad hoc* choices (which is the case for many food webs, e.g. Dommasnes et al. 2001, Ciannelli et al. 2005). Trophic links are then merged following a more-or-less permissive linkage criterion that decides whether to include all or a partial set of the trophic links reaching or leaving the species that were aggregated (Martinez 1993). I tested sensitivity to five linkage criteria. Linkage criteria were selected based on their permissiveness: ‘maximum linkage’ only needs one link between members of each groups to identify a link between trophospecies, whereas ‘minimum linkage’ will only link trophospecies if every members of one group were linked to every members of the other group; I also defined three intermediate linkage criteria (intermediate 75%, 50%, and 25%) corresponding to the proportion of members-to-members links needed to consider a link between trophospecies. Each taxon aggregation criterion was combined with all different linkage criteria.



**Figure 4.** Illustration of the two-step aggregation process. On the left: species with similarities (e.g. taxonomic relatedness, similar diet) are identified in the original network and grouped into trophospecies. On the right: the linkage criterion determines how to keep or remove links between groups of species based on which links existed between members of each group.

### 3.3.3. The fourth-corner method and trait web network

In **Paper IV**, I built ‘trait webs’. Trait webs are bipartite networks of interacting consumer-resource traits. Compared to food webs that are unipartite networks (the nodes all belong to the same type of nodes), bipartites are two-mode networks: consumer and resource traits are split into two distinct layers of nodes interacting only with the other layer, but not among themselves. I used the fourth-corner method (Legendre et al. 1997, Dray and Legendre 2008, ter Braak et al. 2012, Dray et al. 2014) to identify associations between consumer-resource traits that may participate in the establishment of trophic interactions. The fourth-corner tests for associations between two matrices (here, consumer traits and resource traits) based on information from a third matrix (here, the interaction matrix containing trophic links). The method tests for two relationships: that the relation between the resource trait composition and the distribution of trophic interactions does not appear at random, which gives that the resource trait composition influences the occurrence of interactions, and the corresponding for the consumer trait composition. If both consumer and resource trait composition influence the distribution of trophic links in a similar manner, we interpret this as significant associations among consumer and resource traits. The fourth-corner consequently returns an association matrix that can be used to represent interactions between consumer and resource traits as part of a bipartite network: the trait web (Fig. 5). I then used the trait webs to further investigate the trait structure of communities, and assess, e.g., whether there are groups of more closely interacting traits, or modules, in the network.



**Figure 5.** Flow of the conversion process from a food web to a trait web. Trophic link information is inserted as a reduced binary matrix **A** that binds information between consumer and resource trait matrices **B** and **B'**.

### 3.4. Numerical approaches, statistical tools and techniques

In my PhD thesis, I have combined several techniques from network science and graph theory (**Papers I, II, III, IV**), time series analysis (**Papers I and II**), algorithms and modelling (**Papers I, II and III**), as well as univariate and multivariate statistics (**Papers I, II, IV**). Graph theory and ENA allow the analysis of graphical objects such as networks where species are represented as nodes connected by links (here, trophic interactions). Combined with algorithms and other tools from statistics, network analysis makes a powerful tool to describe ecological communities and assess their structure and function over space or time. All analyses were conducted in R (R Core Team 2021) using the base packages, or packages listed below. All network analyses and food web metrics were either coded by myself or co-authors, or computed using the *igraph* package in R (Csárdi and Nepusz 2006).

In **Papers I and II** that investigated the temporal variation in food web structure and function, I constructed time series of food web metrics by building yearly snapshots of the networks. To select species and trophic links, I subsampled from the metawebs using a time-series of species abundances or biomass (ecosystem survey data). Because sampling differed across taxa and years, samples were standardized using a combination of bootstrapping (100 and 1,000 resampling, respectively), data transformations (in **Paper I**, log-transformation and normalization by the mean; in **Paper II**, brought under the same unit of biomass in grams of wet weight per m<sup>2</sup>), and time series analysis techniques (e.g. moving average). The procedures allowed us to create continuous and comparable time



series of abundance or biomass, which were used to extract yearly snapshots of food webs. I then performed the temporal analysis of the food web structure and function by calculating unweighted, node-weighted, and link-weighted metrics for each yearly snapshot of the food webs. In **Paper II**, the temporal analysis of structural metrics was complemented with a principal component analysis (PCA) on the median values of each metric to identify the main temporal dynamics in structure and function, and constrained hierarchical clustering analysis on the scores of the PCA to identify periods in the temporal dynamics (*rioja* package, Juggins 2020).

In **Paper III**, I built algorithms and gradually aggregated a comprehensive food web of the Barents Sea into less resolved counterparts to study the behavior of structural metrics against three aggregation procedures and five linkage criteria. With the taxonomic aggregation, species were lumped together based on their taxonomic information. The structural equivalence aggregation used a modified version of the Jaccard similarity index to aggregate species based on their trophic links in the food web, giving more weight to the prey component, often better determined than the predators (0.6 for the prey and 0.4 for the predators). I grouped species into trophospecies using the  $\beta$ -flexible hierarchical agglomerative clustering (Legendre and Legendre 2012,  $\beta = -0.25$  for balanced grouping). The regular equivalence aggregation was performed with the CATREGE algorithm (available in the *sna* package, Butts 2008) which measures similarity based on the position of species in the food web. Species were aggregated using the  $\beta$ -flexible hierarchical agglomerative clustering with  $\beta = -1$  that favours a complete linkage. I aggregated trophic links using five linkage criteria of increasing permissiveness. For each version of the food web and each technique, I calculated commonly used structural metrics. The clustering was performed using the 'agnes' function from the *cluster* package (Maechler et al. 2016).

In **Paper IV**, I converted food webs into a bipartite network of consumer-resource traits—trait webs—using the fourth-corner method to identify significant interactions between consumer and resource traits (*ade4* package, Dray and Dufour 2007). All traits were converted to categorical traits prior to the analysis to fit requirements of the method. I tested trait associations using model type 6 that reduces false positives, and the  $X^2$  statistic with 100,000 permutations. Additionally, I corrected p-values for multiple testing using the false discovery rate method (FDR, Benjamini and Hochberg 1995) as recommended by Dray et al. (2014). I built and analysed bipartite networks using bipartite graph theory (*bipartite* package, Dormann et al. 2008, Dormann et al. 2020). I aimed to detect modules of more connected consumer-resource traits that could help identify profiles of consumers and resources. I selected the DIRTLPAbw+ community detection algorithm by Beckett (2016) which more consistently detects modules on weighted interactions (here, by frequency of occurrence of consumer-resource

trait relationships). I conducted a similarity analysis of the modules across habitats based on trait category presence/absence using the Jaccard distance (*ecodist* package, Goslee and Urban 2007, 2020).

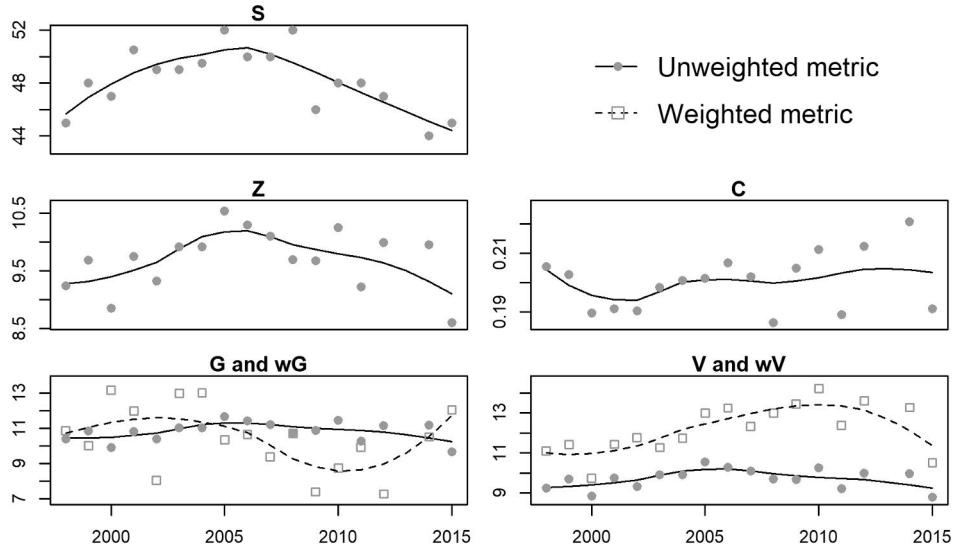
In **Papers I** and **IV**, I complemented the network analysis with community analyses to identify differences in structure (species composition, trophic links, or trait composition) across habitats. I analysed dissimilarity in species composition and trophic interactions by calculating the temporal  $\beta$ -diversity between food web snapshots or habitats (**Papers I** and **IV**, respectively; *betalink* package, Poisot et al. 2012). In **Paper IV**, dissimilarity in trait composition was calculated as the Jaccard distance on the presence-absence of modalities in respective communities (*ecodist* package, Goslee and Urban 2007, 2020).

## 4. RESULTS AND DISCUSSION

My thesis has a two-fold aim: in **Papers I and II**, to explore the temporal variability of food web structure and function, and describe the food web dynamics (species composition, trophic links, abundance, fluxes); and in **Papers III and IV**, to tackle long-standing issues in the building of food webs (aggregation, description of species traits interacting through trophic links). In the first two papers, I show that food web structure and function vary over time. To disentangle food web shifts originating from changes in species presence and absences from changes in the quantities of each species (abundance or biomass), we developed several quantitative counterparts to existing qualitative food web structural metrics. The joint use of qualitative and quantitative metrics revealed complementary information of temporal variation in food web structure. **Paper I** revealed that food web structure not only varies following changes in species composition or trophic links (detected with topological metrics), but also following changes in the dominance of species (detected with node-weighted metrics). **Paper II** further stressed the importance of adopting a complementary approach when studying temporal food web variation. Using a quantitative, flux-based approach, we showed that shifts in food web structure can also emerge as changes in ecosystem functioning, which we were only able to detect with the appropriate methodology. Overall, the results of **Paper I and II** show that temporal changes in food web structure can be linked to underlying changes in species composition, species dominance, and energy fluxes, and that a complementary approach facilitates the assessment of multiple types of change. The second set of questions in the thesis aimed to improve the building and interpretation of food webs. **Paper III** revealed that food web structural properties react unevenly to aggregation. Moreover, not all aggregation procedures perform equally well at maintaining food web structure. Rather, aggregation based on taxonomic relatedness or trophic similarities performed best until food webs were aggregated to about one-fifth of their original complexity. Last, **Paper IV** emphasizes the need to go beyond the concept of species if we want to build more practical representations of food webs. I found that community composition and food web structure differ along a continuum determined by the characteristics of habitats and the traits shared by the species living in those habitats. These results imply that habitats with similar characteristics share similar ecological roles through species biological traits and food web structure. The modularity analysis of the trait webs revealed that trait modules position along the basic vertical organization of food webs into trophic levels, such that the consumer-resource traits within modules represent a certain type of consumer-resource trophic interaction.

#### 4.1. How food webs vary over time: two case studies

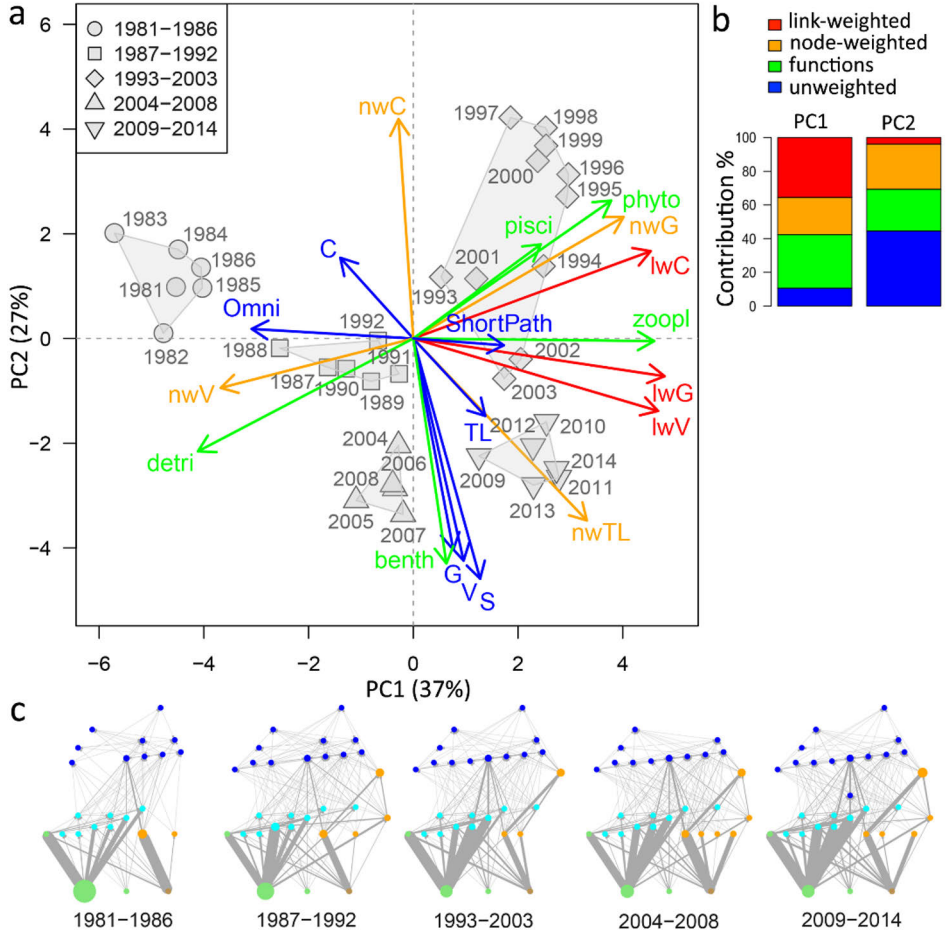
We assessed temporal changes in food web structure and function in two case studies (the German Bight in **Paper I**, and the Gulf of Riga in **Paper II**). Our results highlight that the trajectory of food web structure over time is not linear, but rather that we can observe periods with distinct or transitioning food web structure and function. Our analyses showed that the observed temporal changes in the food web were related to one or more underlying shifts in the community (changes in species composition and the associated changes in trophic links, species abundance or biomass, and energy fluxes).



**Figure 6.** Time series of example food web metrics. From left to right: species richness of the food web (S), link density (Z), directed connectance (C), generality and node-weighted generality (G and wG), vulnerability and node-weighted vulnerability (V and wV). The lines are the LOESS smoothing of the time series on the annual median bootstrap values.

In **Paper I**, we identified two major periods in the German Bight time series (1998-2015). The periods showed distinct food web structures pre- and post-2005, with shifts in values of different food web structural metrics around 2005 (Fig. 6). The first period showed an increase in species richness of the food web (S), further seen in moderate increases in link density (Z), generality (G), and vulnerability (V). In the second period, species richness decreased and the other metrics returned to values similar to what they were prior to the increase in species richness. Directed connectance (C) showed a different pattern with decreasing values in the beginning of the time series, followed by an increase in variability. Abundance-weighted metrics (wG and wV) only followed changes in their unweighted

counterparts prior to 2005, after which, wG showed an accentuated decrease, and wV showed an increase.



**Figure 7.** (a) PCA biplot of the food web metrics summarising the temporal dynamics in food web structure and function (see the time series of metrics in Fig. 2, **Paper II**). Shaded grey areas define the convex hull of clusters of years with similar food web properties. Approaches are displayed with arrows of different colors: in blue, qualitative metrics; in orange, node-weighted metrics; in red, link-weighted metrics; and in green, food web functions. (b) The contributions of each approach to the variance captured by PC1 and PC2. Metrics' abbreviations are described in Table 1 of **Paper II**. Functions are: detri = percentage of detritivory, phyto = percentage of phytoplanktivory, zoopl = percentage of zooplanktivory, and pisci = percentage of piscivory. (c) Illustrations of the time series of food webs showing average link-weighted food web topologies. The time periods were determined by hierarchical clustering on the year scores of PC1 and PC2. The width of trophic links is proportional to the magnitude of energy fluxes.

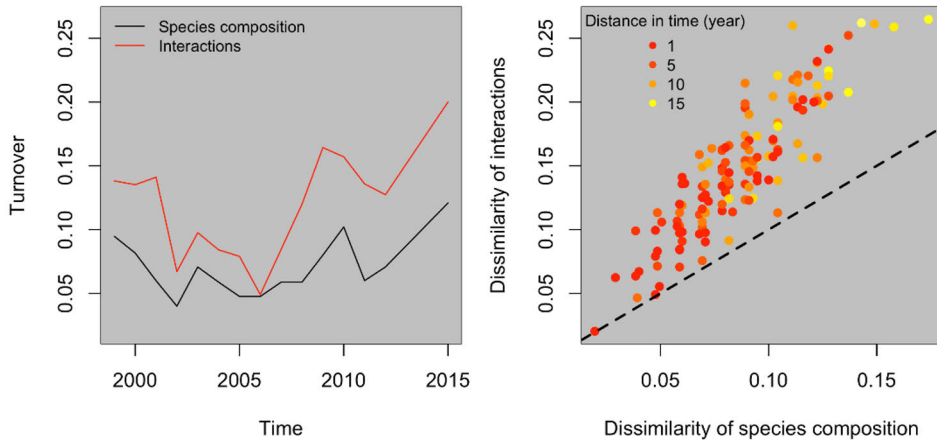
In **Paper II**, we distinguished five periods with distinct food web properties in the Gulf of Riga, i.e. 1981–1986, 1987–1992, 1993–2003, 2004–2008, and 2009–2014 (Fig. 7c). We applied a principal component analysis (PCA) on the metrics to capture the dynamics of the food web structure. The distinction between periods originates from the constrained hierarchical clustering of year scores (the coordinates of years in the PCA space) of the first two principal components. As shown in Figure 7, weighted metrics drove most of the temporal variation (37%, captured by PC1), whereas unweighted metrics represented a consequent secondary source of temporal variation (27%, captured by PC2).

#### 4.1.1. Changes related to shifts in species composition

**Paper I** shows that different species composition can give rise to similar food web structures. The increase in species richness in the German Bight food web (S), associated with an asynchronous increase in directed connectance (C) after year 2000, showed that species added to the food web in the first period of the time series were species with a high total number of links. In **Paper II**, unweighted metrics identified a sudden increase in species richness (from ~20 taxa to about 30 taxa, see time series in Fig. 2 of **Paper II**) with an increase in the length of the food chain (ShortPath) during the third period (1993–2003). In **Paper II**, before 1995, connectance showed less variability compared to species richness, until it drops after 1995, and shows a trajectory opposite of the one of species richness. By definition, connectance is expected to decrease if the number of links and species richness increase linearly (May 1972). However, connectance can increase if the number of links increases faster than the number of species, in other words if the proportion of link to species ( $Z$ ) increases. In **Paper I**, connectance is allowed to increase because species with a higher number of prey (increase in generality,  $G$ ), or which would increase the diet breadth of species present in the food web (increase in vulnerability,  $V$ ) are added to the food web in the first period of the time series. In the second period, connectance remained high and possibly continued to increase because those highly connected taxa remained as others were removed from the food web. On the contrary, in **Paper II**, the changes in generality and vulnerability mirror the trajectory of species richness, but the species present probably have too few interactions (as seen by the low generality and vulnerability) to reverse the trend in connectance. In the second half of the time series, the species present and added to the food web share so few trophic interactions that the complexity drops.

In **Paper I**, our analysis of community dissimilarities across time showed that communities at the beginning and at the end of the time series showed strong differences in species composition and species interactions, despite similar food web structure. Indeed, the turnover of species increased after 2005, and the further apart in time, the more dissimilar food webs were (Fig. 8). In fact, species that contributed to the increase in generality did not necessarily get replaced in

the community, but rather the proportion of generalist to specialist taxa shifted after 2005. During the first period, species with a high number of interactions, and especially a high number of prey, were becoming more and more frequent, when predominantly absent at the start of the time series: *Platichthys flesus*, *Scophthalmus rhombus*, and *Hippoglossoides platessoides* with respectively 28, 24, and 26 prey taxa. However, despite the addition of such generalists to the food web, the proportion of generalist-to-specialist species gradually shifted in the second period due to the intermittent losses of other generalists (e.g., *Gadus morhua* with 46 prey). In the Gulf of Riga, Pecuchet et al. (2020b) documented a structural and functional reorganization of the ecosystem. In **Paper II**, following the disappearance of *G. morhua*, a high generalist consumer, from the area, other species became more dominant, such as small and more specialized planktivorous fish like sprat (*Sprattus sprattus*) and herring (*Clupea harengus*).



**Figure 8.** *Left panel:* Dissimilarity of species composition and trophic interactions between food webs of consecutive years. *Right panel:* Relationship between dissimilarity of species composition and dissimilarity of trophic interactions for all pairs of food webs. The colour gradient indicates the time distance between food webs. (Paper I).

#### 4.1.2. Changes related to shifts in species dominance

Shifts in relative abundances are not necessarily seen in unweighted metrics describing food web structure but they can have a strong influence on how we interpret trophic architecture. Node-weighted metrics (e.g. node-weighted generality, wG) can both highlight changes in the topological structure and in the abundances of taxa. **Paper I** and **II** showcase examples of the complementarity of node-weighted metrics to purely binary descriptors. For instance, in the German Bight time series (**Paper I**), before 2006, node-weighted metrics displayed temporal trajectories similar to unweighted metrics (e.g. vulnerability V and wV,

Fig. 6). However, later deviations between these metrics revealed changes in species dominance (after 2006 for wG and wV), when species like the brown shrimp (*Crangon crangon*), or the Atlantic mackerel (*Scomber scombrus*) were supplanted by other, dominant species (*Crangon allmanni*, *Sprattus sprattus*, *Clupea harengus*, Fig. 6, and see time series of abundance anomalies, Fig. 5, **Paper I**), or may have migrated away from this area (e.g., northerly migration of the horse mackerel, *Trachurus trachurus*, Reid et al. 2001). These changes in dominance are in line with earlier observations that pelagic piscivores and planktivorous fish were supplanting benthivorous fish (over 1973–2000, Heath 2005). **Paper II** similarly showed complementary information from weighted vs. unweighted metrics as seen in the lack of correlation between weighted and unweighted metrics (Fig. 7a-b) and the diverging trajectories of unweighted and weighted counterparts (see time series of metrics in Fig. 2, **Paper II**). Along with a sudden increase in species richness, some species also increased in number: here, an increase in biomass of pelagic fish such as *Sprattus sprattus* and *Gasterosteus aculeatus*; zooplankton such as *Eurytemora affinis* and *Acartia* spp.; benthos such as *Pontoporeia affinis*; and non-indigineous species *Marenzelleria* spp. and the round goby, *Neogobius melanostomus*. These changes in species composition and increases in the number of some species (abundance or biomass) could be linked to the various anthropogenic pressures in the Baltic Sea (Reusch et al. 2018) that may favour population growth of some species (stickleback, Bergström et al. 2015) and introduction of others (round goby, Ojaveer et al. 2017).

Node-weighted metrics do not integrate the dynamics of the system through the means of dynamical equations (unlike models like ‘Ecopath with Ecosim’, Skaret and Pitcher 2016) that estimate abundance or biomass for the next time step. However, they can act as a proxy for the dynamics occurring between time-steps: abundance or biomass is the net sum of births, deaths, immigrations, and emigrations. Node-weighted metrics alone can be somewhat challenging to decipher, however the comparison of unweighted and node-weighted metrics can help disentangle which dynamics originate from changes in species composition and which originate from changes in species quantities (abundances, biomass). When unweighted and node-weighted metrics follow the same dynamics—similar direction and amplitude of change, despite differences in their range of value—I argue that the observed dynamics represent changes in species composition and associated trophic links, or at least that the changes in species composition and trophic links outpace any changes in relative numbers. Similarities in behaviours of node-weighted and unweighted metrics can suggest a rebalancing of trophic interactions through fluctuations in quantities of each species and shifting in species dominance so that node-weighted metrics change along with unweighted counterparts (asynchronization of resources, McMeans et al. 2015). When unweighted and node-weighted metrics deviate from one another, however, changes in numbers happen at a magnitude much greater than changes in the



topological structure, which can even reverse patterns observed for unweighted metrics. Such changes may suggest a trophic reorganization of the food web that could impact ecosystem functioning. An additional analysis on the dynamics of each species can help identify which species are responsible for the observed dynamics.

#### **4.1.3. Changes related to shifts in energy fluxes and ecosystem functioning**

In the previous sections, I observed that taxonomically differing assemblages could lead to similar trophic structures. An important question is whether such species assemblages will lead to similar levels of ecosystem functioning. **Paper II** illustrates the multi-trophic temporal reorganization of the Gulf of Riga food web, and the changes in functioning (Fig. 7). At first, the food web was largely dominated by detritivorous flows (1981-1986), then shifted towards an increasing proportion of pelagic and planktivorous flows (1987-1992), as shown by the flows and the separation between the early and late years along PC1. In the early 1980s, the cold winters with sea ice (Einberg et al. 2019) probably favored a community dominated by detritivorous flows, with organisms exploiting decaying sea ice algae. We presume that deposition of sea ice diatoms (Arctic diatoms, Jurgensone et al. 2011) may have fueled under-ice benthic production. The subsequent milder winters (with no ice) in the 1990s, however, likely favoured warm-water zooplankton, associated pelagic predators (e.g. herring), and overall pelagic-dominated community as shown by increased phytoplanktonic and zooplanktonic fluxes (e.g. copepod *Eurytemora affinis*, Livdāne et al. 2016, and herring, Ojaveer et al. 1999). A similar trophic reorganization, from a benthic-dominated to a pelagic-dominated food web, was observed in the central Baltic Sea following a regime shift which led to small pelagic predators such as sprat to dominate the ecosystem (Möllmann et al. 2009). The decrease of *Gadus morhua* in the main basin extended to the Gulf of Riga, and using a flux-based approach, we were able to follow progressive changes in the functioning of the ecosystem, which otherwise could have been left unobserved using unweighted metrics alone. Möllmann et al. (2009) suggested the in-between years (1987-1993) to be regarded as a transition period. In **Paper II**, it seems transition periods correspond to periods when unweighted and node-weighted metrics showed the largest mismatch. It is possible that transition periods could be characterized by higher magnitude of changes in species quantities (abundance or biomass) than changes in species composition, which could lead to a trophic reorganization, without a complete loss of species.

#### **4.1.4. Complementarity of food web qualitative and quantitative metrics**

The temporal analyses of the German Bight and Gulf of Riga food webs revealed changes in food web metrics over decadal time series. We identified periods that were characterized by distinct metrics. Whereas some (qualitative) metrics showed moderate changes, other (quantitative) metrics showed stronger fluctuations. Unweighted, node-weighted, and link-weighted food web metrics highlight different and complementary aspects of food webs temporal variability. Using one method rather than another may lead to incomplete conclusions. Rather, metrics should be selected for the complementarity of what they describe. Unweighted metrics describe macroscopic aspects of the food web structure but can sometimes appear stable over long periods of time (e.g. unweighted connectance, number of links, Trøjelsgaard and Olesen 2016), despite evident fluctuations in weighted metrics indicating community change. On the other hand, node-weighted metrics can highlight when the source of variation is related to changes in dominance of species. While topological and node-weighted metrics analyze the influence of the nodes on the network rather than the links (i.e. giving equal weight to all links), link-weighted metrics can help identify how information travels throughout the network (e.g. where fluxes of matter go, which pathways are more influential for the robustness of the network). For instance, we noticed that link-weighted metrics had generally lower values than if all links would have the same weight (so equal to unweighted metrics). It shows that in- and out- flows are not equally distributed across species. Rather, they show a skewed distribution with many species sharing weak fluxes, and a few sharing strong fluxes. A quantitative analysis of the fluxes can help identify how changes in the structure may affect the functioning of the food web. When analyzing any type of variation in food webs (spatial or temporal), I suggest that we select unweighted and weighted metrics for their complementarity because they can (i) highlight different drivers of change (species composition, shift in dominance, multitrophic reorganization with changes in ecosystem functioning), and (ii) are thereby more likely to identify periods (and transition periods) of change.

#### **4.1.5. Food web topologies and their limitations**

**Paper I** and **II** are examples of food web studies where we explore the dynamics in the nodes (presence/absence, dominance) and in the links (energy fluxes) of the topology. Typical dynamical food web models are built upon dynamic equilibriums assuming mass-balance between the different actors of the food web, and use mathematical equations that are often difficult to parameterize at the scale of ecosystems ('Ecopath with Ecosim', Skaret and Pitcher 2016). The challenging parameterization and high computational demands often lead to simplifications either regarding the complexity of the underlying food web topology (i.e. food web aggregation, McCormack et al. 2017) that may alter the structure of the food web.

The approach in this thesis, however, does not use empirical data to feed a model, but rather considers empirical observations (abundance or biomass) as the net sum of natural yearly dynamics, which is then reflected in the topology. By doing so, we assume that the size of consumer and resource populations are changing over time, and that those fluctuations should be reflected in our estimations of food web structure. Furthermore, weights to the links (e.g. fluxes) and link-weighted metrics should not be discarded. When the size of food webs allows for their computation, weight to the links (e.g. fluxes) inform on the functioning of food webs.

The results presented in my thesis come with several assumptions and limitations. First, we assumed that trophic interactions are solely driven by species composition. We know that trophic interactions may well be context-dependent (Poisot et al. 2015). Improvements on the study of variation in the structure of food webs will need to allow for rewiring of trophic links to provide accurate analysis of food web structure over space or time (Thierry et al. 2011). Second, we assumed that trophic interactions occurred based on neutral processes, and that abundances (or biomasses) would represent adequate proxies to estimate how the food web structure varies over time. This simplification assumes no individualistic behavior, and that each individual of a species has the same potential of realizing the trophic interactions seen at the species level. Thus, node-weighted metrics estimate the structure representing a scenario in which each individual of the resource species will form the same combination of trophic links with each individual of the consumer species. Nonetheless, in nature, we expect individuals to differ in how they decide to use their habitat or acquire their food, ultimately leading to differences in vulnerability to predators and prey selection (Pettorelli et al. 2011).

## **4.2. How to build more realistic and practical food webs**

In the second part of my thesis, I explored two aspects of building food webs. First, how to aggregate species and their trophic links into less complex food webs that retain structural properties of more complex counterparts (**Paper III**). I showed that some methodologies perform better at maintaining food web structure. I discuss procedures and provide guidelines on how to aggregate food webs. Second, I compare four local food webs to investigate similarities and differences in communities and food web structure at the local scale (**Paper IV**). I found that species composition and food web structure differ along a continuum where habitats sharing characteristics (vegetated vs. unvegetated) and communities harboring species with similar adaptations (traits) seemingly share higher similarities in food web structure. Then, I studied the building blocks of food webs, and explored how interactions between consumer-resource traits arise through food web structure. I found that some associations of consumer-resource traits

occur more frequently across habitats, whereas others are specific to certain habitats.

#### **4.2.1. How to aggregate taxa and their trophic interactions**

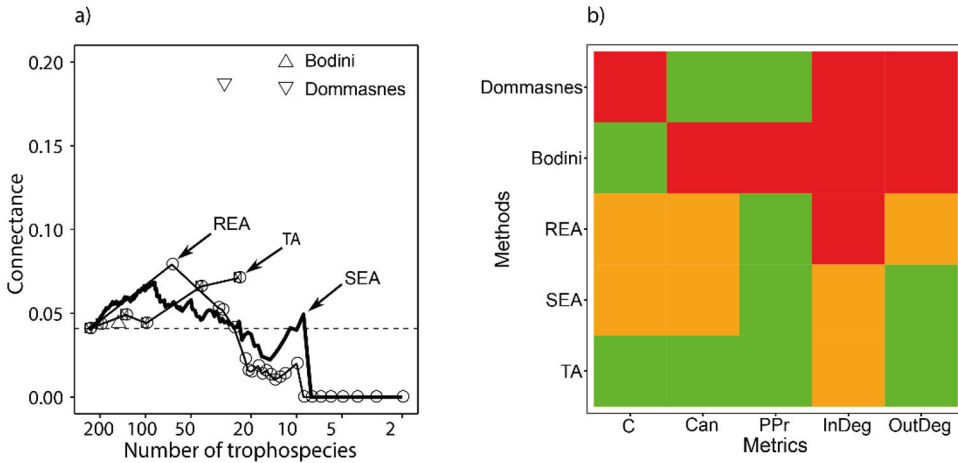
How we aggregate and simplify food web representations can alter the food web structure and distort our understanding of the food web structure. To aggregate food webs, it is necessary to consider two steps: how to aggregate taxa, and how to aggregate their links. In **Paper III**, I tested the sensitivity of food web structural properties to a combination of three taxa aggregating methods and five linkage criteria, and the capability of each aggregation protocol at maintaining the food web structure. I found that not all food web structural properties are as robust to aggregation, and that not all aggregation protocols perform well at maintaining the food web structure (Fig. 9). From the initial analysis of linkage criteria, I found that an intermediate 25% linkage is most effective at retaining food web structural properties. Food web metrics departed rapidly and strongly from original values using other linkage criteria: they were either too permissive (e.g. maximum linkage), or too restrictive (intermediate 50%, 75%, and minimum linkage). Therefore, I present the sensitivity of food web structural properties to aggregation methods following an intermediate 25% linkage criterion.

The directed connectance of the Barents Sea food web (Planque et al. 2014) is 0.040 (4% of all possible trophic links are expressed). This value is set as reference to evaluate the sensitivity of directed connectance to aggregation procedures. Connectance tended to rise away from the reference for aggregation steps that would reduce the food web down to ca. 30 trophospecies. For higher levels of simplification, connectance would fall below the reference, ultimately reaching values typical of fully disconnected food webs (i.e. 0). Exploring other metrics, I found that no aggregation procedure would strictly maintain the original values, but rather, values would oscillate around the original reference as species and their links get lumped together. As such, the best performing method will be the method that oscillates the closest to the original value, and that allows the highest level of simplification without altering too much the original food web structure. I found that overall both taxonomic and structural equivalence aggregation procedures performed best at maintaining the food web structure. Metrics were slightly more robust to taxonomic aggregation, however, structural equivalence aggregation allowed for a more gradual and progressive lumping of species that was needed to reach higher levels of aggregation. Using structural equivalence aggregation, I found that I could reduce the Barents Sea food web topology from 233 trophospecies down to about 30-60 trophospecies, while still maintaining its food web structure.

Martinez (1993) showed that passing a certain threshold, food web structural metrics become highly sensitive to subsequent steps of aggregation. How and

when structural properties depart from original values may signal when to stop aggregation: beyond such a threshold, aggregation procedures can no longer maintain the structure of the food web. By pushing the aggregation too far, we possibly start lumping species with distinct ecosystem roles (e.g. merging across trophic levels, or across functional groups). The two best-performing methods involved either morphological similarities (taxonomic aggregation), or trophic similarities (structural equivalence) where consumers in each group most likely target taxa with similar morphological characteristics, and hold similar morphologies for the trophospecies that preyed upon them. An explanation behind such higher performance could be that, generally, species with related taxonomies display similar biological traits, which are thought to rule the occurrence of trophic interactions (trait matching rules, Bartomeus et al. 2016). Similar traits could mean similar trophic interactions within the food web, thus lower sensitivity to aggregation procedures for methods that rely directly or indirectly on similarities in biological traits.

My results show that aggregation procedures should be chosen with care, and reported, if we want to ensure comparability across studies. A previous study showed that dynamic models displayed differing structure and dynamic stability based on how aggregation was performed (Pinnegar et al. 2005). Food web modelling is an essential tool to investigate the structure and dynamics of ecosystems, or to provide guidance on ecosystem management. Multiple attempts have been made to describe the food web structure: from phenomenological models such as the 'niche model' (Williams and Martinez 2000), to mechanistic models such as the 'evolutionary food-web model' (Loeuille and Loreau 2005). Other models build upon food web topologies in order to model the food web dynamics: for instance, Ecopath models such as the Barents Sea model (Dommasnes et al. 2001), or the North Sea model (Mackinson and Daskalov 2007). To date, any of these models are limited in how much complexity they can incorporate, which often requires aggregation of more complete topologies. Considering the sensitivity of models and topologies to aggregation procedures, I propose to use aggregation as a preliminary evaluation step, rather than simply apply aggregation to fit requirements of models. Structural equivalence aggregation (with the intermediate 25% linkage) could be used to diagnose the effect of aggregation of the model, and identify the limits of the aggregation.



**Figure 9.** Sensitivity of the Barents Sea food web to aggregation according to three procedures and intermediate 25% linkage criterion: Taxonomic Aggregation (TA), Structural Equivalence Aggregation (SEA), and Regular Equivalence Aggregation (REA). Figure 9a shows performance of each method at maintaining directed connectance. The horizontal dotted line indicates the value computed for the original food web of Planque et al. (2014). Strong and early departures from the original connectance show poor capabilities of the method at maintaining the food web structure. Connectance of the Bodini and Dommasnes' food webs are given as reference (upward and downward triangles, respectively; Bodini et al. 2009, Dommasnes et al. 2001). Figure 9b shows performances of each method at each of the food web structural properties (in abscisse, from left to right, directed connectance, cannibalism, predator-prey ratio, dispersion of in-degrees, dispersion of out-degrees). Green: most values stay within  $\pm 25\%$  of the original value; the method maintains the food web structure property very well. Orange: most values stay within  $\pm 25\text{--}50\%$  of the original value; the method slightly alters the information provided by this property. Red: most values are beyond  $\pm 50\%$  of the original value; the information provided by this property is lost.

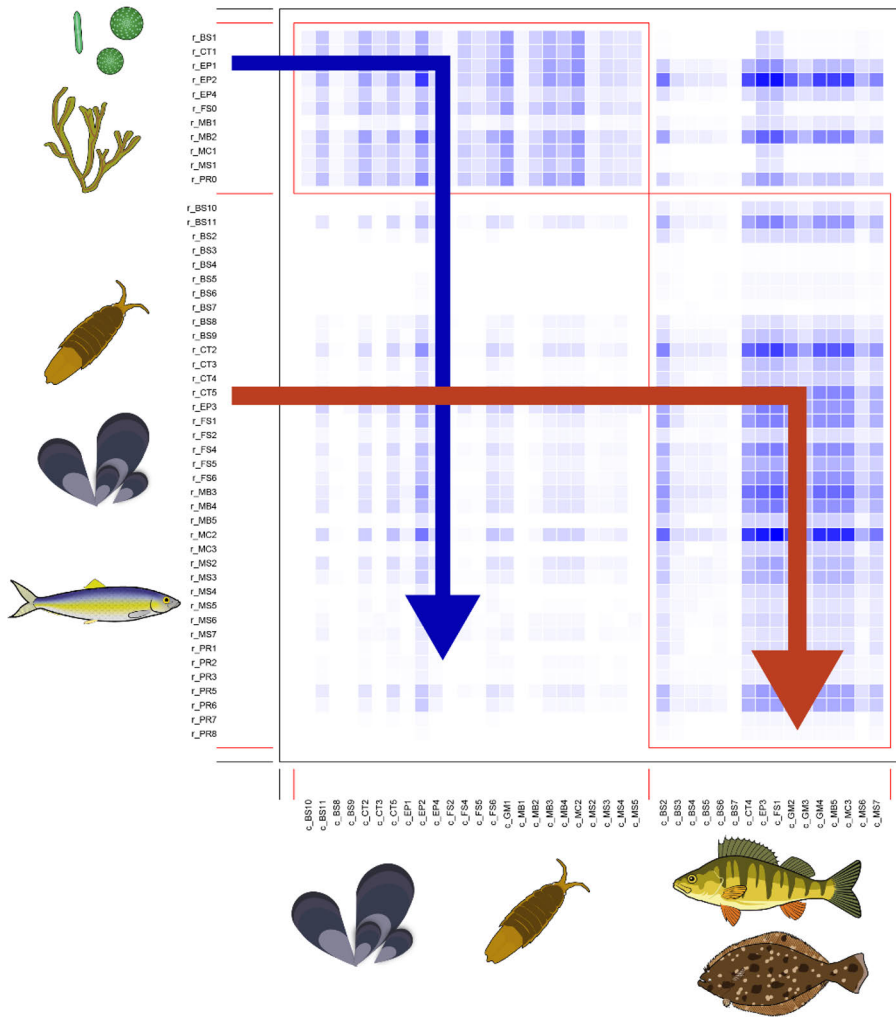
### 4.2.2. Biological traits at the service of food web science

**Paper IV** emphasizes the need to go beyond species taxonomy by identifying consumer-resource trait associations that occur more frequently than expected in nature. I first compared the structure and composition (species, trophic links, and traits) of four habitats (*Fucus*, *Zostera*, sand, rock). I then used the trophic interactions to quantify the frequencies of consumer-resource trait associations. I found that local communities differed much more in terms of the composition of species and trophic interactions, than in terms of trait composition. At the local scale, food web structure varied along a continuum where habitats sharing characteristics of complexity (e.g. presence of vegetation, bare bottoms) were more similar than otherwise. Similar habitats are likely to harbour similar species, and more complex habitats more complex communities. A reason could be that elements of habitat complexity, such as vegetation, diversify the niches available for species to occupy: in habitats of higher complexity, some species will be able to fully utilize the habitat, while others will be constrained to some parts (e.g. sand in *Zostera marina* patches). A similar pattern appeared in the analysis of significance of consumer-resource trait associations. While some consumer-resource trait association are found in all habitats ('ectotherm vertebrates' feeding on 'invertebrates', or the gut morphology of invertebrates with the body size, body shape, and other trait modalities characteristic of phytoplankton), most trait associations are either specific to a habitat, or shared across pairs of habitats when those share characteristics. For instance, in the *Fucus*-habitat, some 'obligate swimmer' species fed on 'primary producers', whereas the association involving crawler-burrower consumers and primary producers was significant in both vegetated habitats.

Whether organisms will be able to withstand the abiotic and biotic conditions of new or changing environments will depend on the response traits they are equipped with (Díaz et al. 2013). This may explain why organisms may be constrained to specific habitats or regions, thus leading to differences in species composition and species interactions. Research has shown that food webs do not assemble at random but rather follow a set of rules that explain their robustness to perturbations over time (Cohen et al. 1985, Williams and Martinez 2000). Several studies have demonstrated that the structural patterns observed in empirical food webs can be reproduced from a limited combination of traits: for instance, body mass is often a good predictor since consumers that swallow resources whole are often larger than the resource itself (e.g. Eklöf et al. 2013, Pomeranz et al. 2019, Brose et al. 2019). Few studies took the opposite approach of linking consumer-resource traits based on observed trophic interactions (e.g. Spitz et al. 2014, Laigle et al. 2018, Monteiro and Faria 2018). In **Paper IV**, the analysis of modularity in consumer-resource trait webs showed that consumer-resource trait associations capture the vertical structure of food webs along distinct trophic levels (primary producers being consumed by ectotherm

invertebrates, themselves consumed by ectotherm vertebrates). Additionally, modules of consumer-resource associations identify clusters of resource traits that interact more closely with specific clusters of consumer traits. For instance in the *Fucus*-habitat (Fig. 10), the smaller module described traits typical of phytoplankton species (the resource, with trait modalities such as size “XS”, “passive-floater”, or “plant-like” body shape), interacting closely with traits typical of small to medium invertebrate feeding on particles in the water (the consumer, with trait modalities such as “articulate” or “bivalve” body shapes, “grazer” or “filter-feeder”). Traits within clusters are more likely to be shared by the same profile of interactors, which we could use to portray interacting organisms: what characteristics does A have when it is known to interact with B? What characteristics does B need to interact with A? Expanding this analysis to larger datasets (such as in Monteiro and Faria 2018) should help identify and refine consumer-resource profiles. The results of **Paper IV** echoes that of **Paper III** that species with similar traits (e.g. part of the same genus) will likely be involved in similar types of trophic interactions, or interacting with similar species. It comes with less surprise that methods directly or indirectly aggregating species with similar biological traits would give the best performance.





**Figure 10.** Modules of the predator-prey bipartite *Fucus* trait web. The analysis reveals two modules that describe profiles (i.e. the set of traits) of specific resources and consumers. Examples of resources and consumers in each module are represented as illustrations.

## 5. CONCLUSION

### 5.1. Key findings and implications

First, my thesis shows that food webs are changing over time (**Paper I** and **II**) and that such changes are best identified using a set of multiple, complementary metrics. I show that typical unweighted metrics may remain unchanged despite changes in species composition. Specifically, unweighted metrics capture changes resulting from the loss or addition of species to the community, and are not suitable for following e.g. changes in abundance. In **Paper I**, I developed node-weighted structural metrics that ascribe quantity of species (abundance or biomass) to the nodes of the food web. The joint analysis of unweighted and node-weighted metrics revealed changes in food web structure connected to altered dominance in the German Bight, shifting from benthic and demersal generalist taxa, to a community dominated by pelagic specialist taxa. In **Paper II**, we documented changes in food web structure for the Gulf of Riga over almost four decades. We showed that changes in species composition further impacted the functioning of the food web, and that those changes again were detectable using a set of complementary qualitative and quantitative methodologies.

My thesis highlights that there should be no primacy in which metrics we choose to analyze changes in food webs (structure and function). Rather, qualitative (unweighted) and quantitative (node-weighted, flux-based link-weighted) metrics revealed complementary in our understanding of temporal variation in food webs. The methodology in **Paper I** and **II** presents a way to study food webs using data that has already been collected in monitoring of ecosystems (species composition, abundance). However, monitoring of food webs will only work if we select a set of complementary indicators that inform, both, on the macroscopic and microscopic states of the system (i.e. the system as a whole, and entities, such as taxa, that compose the system). Rapid changes in qualitative and quantitative metrics may signal a reorganization of the community, however, alone, they are poor descriptors of how ecosystems might be changing as a whole. For instance, species abundances may be rebalanced as a result of changing species composition, which can only be revealed by the comparison between unweighted and node-weighted equivalent metrics. Temporal variation in unweighted and weighted metrics can be hard to decipher when analyzed separately, however, their comparison can help disentangle the causes of temporal variation for distinct time periods (species composition, abundance, function).

Being able to build realistic food webs is essential if we want to integrate food webs to the monitoring and management of ecosystems. **Papers III** and **IV** give insight into how to improve our building of food webs. The results of **Paper III** showed that the choices we make when building food webs can drastically alter

the perspectives we have of them. Most food webs used in ecosystem management (e.g. to assess impact of policies) rely on food web models built by different users, thus varied methodologies, and for specific purposes. As such, their topological structure is often inherently biased by the choices of who built them. One common procedure is to aggregate species to either reduce the complexity of a model, or minimize the bias originating from the lack of diet information. My results show that food web structural metrics react differently to aggregation methodologies, and to the level of aggregation. Thus, aggregation procedures should be a conscious choice rather than an educated guess. The results show that methods based on information related to the trait similarities of species (e.g. their taxonomic relatedness, or trophic similarity) should give the best performance at maintaining the food web structure. That is because biological traits seem to be central in how communities are structured (**Paper IV**). The final study in my thesis showed that, at the local scale, food webs structure along a continuum determined by similarities in habitat characteristics. Habitats with similar complexities most likely harbour species with similar response traits, which allow them to spillover to other habitats when those share similar characteristics. Additionally, I analyzed the consumer-resource trait associations behind the observed food web structure. Building networks of traits, I found that trait associations expose the vertical food web structure (trophic levels) into profiles of interacting consumers and resources. Trait profiles describe what typical consumer and resource look like, and can help identify trophic interactions for the purpose of building food webs.

## **5.2. Linking it all together: Limitations and future directions**

Building food webs is a necessary but daunting task: diet information is still lacking for many species; trophic interactions are contextual; ecological communities change over time, and with them the food webs. We will probably never be able to sample the real food web, let alone monitor all the interactions in the food web at high temporal or spatial resolution. If we want to track changes in the structure and functioning of ecosystems, I believe effort should be placed on identifying food web assembly rules, and I believe that consumer-resource trait associations are part of the answer. Eklöf et al. (2013) showed that we can reproduce food web structure using a limited set of traits. Body size rules alone were able to reproduce trophic interactions with great accuracy (Gravel et al. 2013). Species traits hold great promise for understanding interactions because they determine where and when two species will be found (Laughlin et al. 2012, Cadotte et al. 2015), and if they will be able to interact (Eklöf et al. 2013, Bartomeus et al. 2016). Additionally, traits are more practical to collect for several reasons. First, their sampling is easier and less variable than that of food webs: traits can be measured for each individual caught, whereas not all individuals caught will have prey items in their gut. Second,

traits can be recorded for both predators and prey, when trophic interactions are most often recorded from the perspective of the predator. Third, a single trait can hold several pieces of information: why this organism is found in this environment, and with whom it may, or may not, interact. Last, trait information is useful in the process of building food webs (e.g. collecting trophic interactions from the literature based on similar biological characteristics or taxonomic relatedness, inference based on trait-matching, or aggregation of species based on traits).

In my thesis, food web rewiring was not included. Despite theoretical evidence that rewiring might influence the robustness of food webs to perturbation (Thierry et al. 2011), to this day, there is no accurate method to predict which trophic interactions will disappear, and which new interactions will be enabled. Recently, trait-based approaches that used machine learning algorithms showed promising results at determining whether taxa are a good fit as potential interactors (Desjardins-Proulx et al. 2017, Pichler et al. 2020). The method only requires a matrix of interactions (which does not need to be a complete network), and two trait matrices that describe the interactors. Though the analysis was performed on plant-pollinator networks, we already have access to information that can be used to test those algorithms on predator-prey interactions, without the need to build a complete food web (e.g. databases of species interactions such as GloBI, Poelen et al. 2014, and other databases containing trait information such as FishBase, Froese and Pauly 2021). If we can combine what we know of species (e.g. their taxonomy, their biological traits, their known interactions), and train such algorithms to include information that incorporates everything we know of the filtering process, then we would get one step closer to building food web models that adapt to the spatiotemporal context, providing a window into marine ecosystems in the future.

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Pierre Olivier

# **Marine Food Webs:**

## **an Exploration of Past Structure and Function to Prepare for the Future**

This thesis explores how marine food webs—the networks of ‘who eats whom’ in nature—have changed over time, and how we can improve the building, use, and applicability of food webs to prepare for the future.

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