



Predation control of zooplankton dynamics: a review of observations and models

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We performed a literature review to examine to what degree the zooplankton dynamics in different regional marine ecosystems across the Atlantic Ocean is driven by predation mortality and how the latter is addressed in available modelling approaches. In general, we found that predation on zooplankton plays an important role in all the six considered ecosystems, but the impacts are differently strong and occur at different spatial and temporal scales. In ecosystems with extreme environmental conditions (e.g. low temperature, ice cover, large seasonal amplitudes) and low species diversity, the overall impact of top-down processes on zooplankton dynamics is stronger than for ecosystems having moderate environmental conditions and high species diversity. In those ecosystems, predation mortality was found to structure the zooplankton mainly on local spatial and seasonal time scales. Modelling methods used to parameterize zooplankton mortality range from simplified approaches with fixed mortality rates to complex coupled multispecies models. The applicability of a specific method depends on both the observed state of the ecosystem and the spatial and temporal scales considered. Modelling constraints such as parameter uncertainties and computational costs need to be balanced with the ecosystem-specific demand for a consistent, spatial-temporal dynamic implementation of predation mortality on the zooplankton compartment.

Keywords: ecosystem models, regional Atlantic ecosystems, trophic control, zooplankton, zooplankton closure term.

Introduction

Zooplankton, comprising heterotrophic marine plankton including both herbivorous and omnivorous species, forms an important part of marine ecosystems transferring energy from primary production to fish. Within regional marine ecosystems, several processes govern the structure and dynamics of the zooplankton community. Additionally to natural mortality, population growth rates of zooplankton could be subject to either bottom-up control

(resource limitation) or predation by higher trophic levels (top-down control). Global approximations of zooplankton mortality by comparing *in situ* measurements of adult copepods longevity and predator-free laboratory longevity showed that predation mortality accounts for 67–75% of total mortality (Hirst and Kiørboe, 2002). Therefore, predation was more important than other sources such as parasitism, disease, and starvation. Although bottom-up processes are thought to control the seasonal

production cycle in many marine ecosystems, time-series analyses suggest that the top-down control of lower trophic levels (LTLs) can exist, at least during some periods. Frank *et al.* (2006) compared a number of regional ecosystems in the Northwest (NW) Atlantic pointing out that changes in primary productivity, species diversity, and temperature might alter the status of the ecosystem. For quantifying the potential magnitude of top-down control on the zooplankton community, not only the total amount of zooplankton biomass but also the size structure and species composition of the community is relevant, given the dependence of fish critical feeding life stages to a certain prey size spectrum (Beaugrand *et al.*, 2003; Voss *et al.*, 2003; Dickmann *et al.*, 2007; Daewel *et al.*, 2008a). Besides the size-specific predation by higher trophic levels, environmental conditions and intraguild interaction are relevant to structure zooplankton communities. This includes both intraguild competition (Brooks and Dodson, 1965; Hall *et al.*, 1976) and intraguild predation (in this case, grazing of zooplankton on zooplankton) due to the cannibalism of eggs and nauplii (Plourde *et al.*, 2009; Neuheimer *et al.*, 2010) or due to predation from carnivorous zooplankton species such as ctenophores, siphonophores, chaetognaths, euphausiids, and hydromedusae (Hirst *et al.*, 2007).

For better understanding the processes driving plankton dynamics, one of the available tools is to use modelling approaches. Although the history of zooplankton modelling goes back to the 1960s (for a discussion, see, for example, Mullin, 1975), integrative biogeochemical LTL

models (nutrient–phytoplankton–zooplankton–detritus, NPZD) have specifically evolved over the last 30 years (Fulton, 2010), starting with simple NPZ chains (Fasham *et al.*, 1990) and increasing in complexity to include additional limiting nutrient cycles and multiple phytoplankton and zooplankton functional groups (e.g. Skogen *et al.*, 2004; Schrum *et al.*, 2006; Eilola *et al.*, 2009). In the majority of LTL models, the zooplankton compartment(s) typically act(s) as a closure term for nutrient and carbon fluxes, but recent model development have incorporated population or individual dynamics of targeted zooplankton species or groups (Carlotti and Poggiale, 2009). A review of the role and parameterization of the zooplankton compartment in foodweb models has been published by Carlotti and Poggiale (2009). In general, the approach chosen to implement zooplankton in a model (Figure 1) depends on the research interest or the purpose of the model and is heavily influenced by the trophic level of interest. Where models have been developed to understand biogeochemical fluxes and LTL production, zooplankton is usually represented as either a single functional group (Edwards, 2001) or separated into several groups implicitly based on either body size, rates of population turnover, or their feeding preferences including herbivorous, omnivorous, and, in some examples, carnivorous compartments (Oguz *et al.*, 2008; Daewel and Schrum, 2013; Huret *et al.*, 2013). However, the biological traits, which separate these functional groups, are generally poorly described. Another approach places more emphasis on simulating the population dynamics and spatial-temporal distribution of a key species (one that either constitutes the dominant

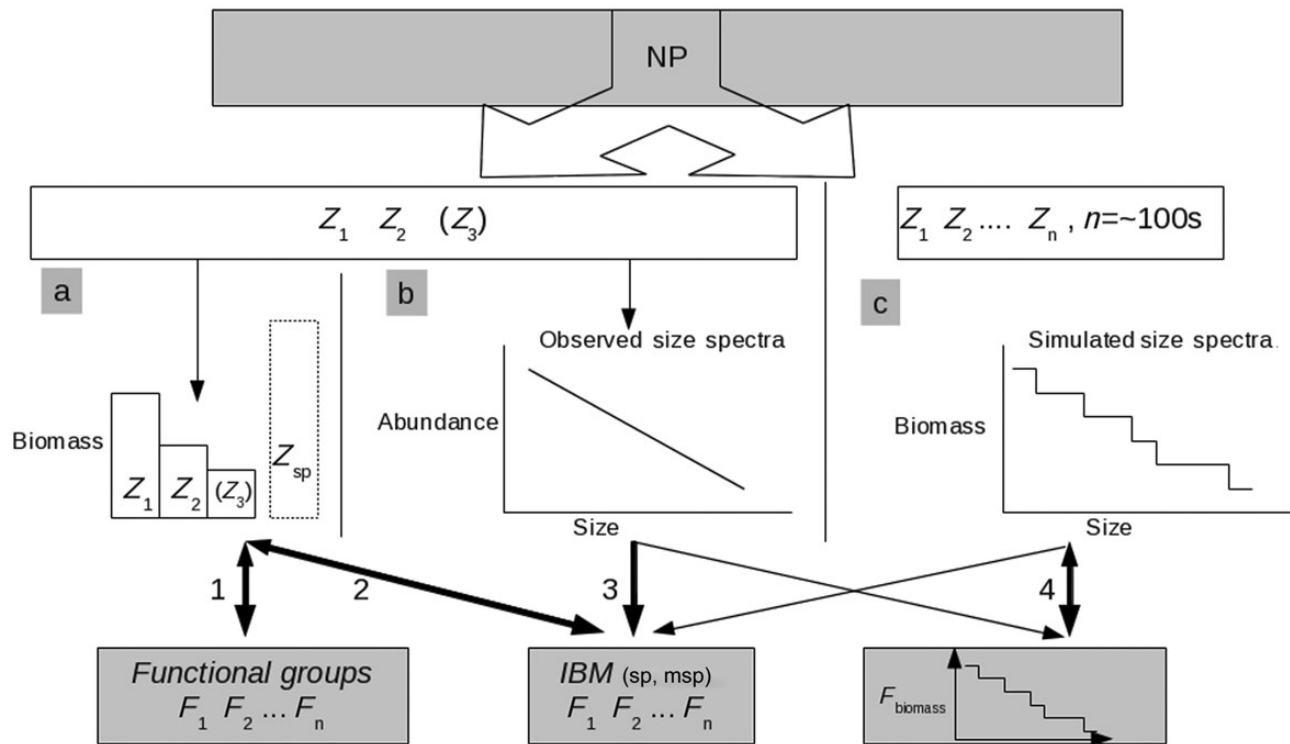


Figure 1. Schematic of the coupling between LTL (Nutrient-Plankton type) and fish (F) models through different zooplankton (Z) formulations: (a) zooplankton is represented as two or three functional types (FT) with potentially an additional dominant single species (Z_{sp}) for which population dynamic is simulated (e.g. Hjøllo *et al.*, 2012); (b) zooplankton FT are transformed into continuous size distribution from available size-spectra data (e.g. Daewel *et al.*, 2008b); (c) zooplankton is dynamically size-resolved (e.g. Baird and Suthers, 2007). Available models for trophic transfer to fish are indicated by bold arrows: (1) Fennel (2008) (single-species groups); (2) OSMOSE (Travers *et al.*, 2009); (3) Daewel *et al.* (2008a); (4) Maury *et al.* (2007). Possibility of one- or two-way coupling is indicated by the arrow direction. Thin arrows indicate other possible links between zooplankton and fish.

zooplankton or plays an important role in structuring the zooplankton community) rather than on the total zooplankton field. This kind of model combines biogeochemical models with either zooplankton population models (e.g. Fennel and Neumann, 2003; Moll and Stegert, 2007; Ji *et al.*, 2009, 2012b; Stegert *et al.*, 2012; Maar *et al.*, 2013) or individual-based models (IBMs; e.g. Hjøllø *et al.*, 2012).

In more recent studies, a number of promising efforts have been made that link size-structured zooplankton models to biogeochemical approaches. Based on the biomass spectrum theory developed by Platt and Denman (1977), Zhou and Huntley (1997) provide a formulation that calculates the slope of the biomass spectra based on demographics and physiological properties. In Zhou *et al.* (2010), the same authors present a size-spectrum zooplankton closure model that can be linked to every NP model. In Maury *et al.* (2007) and Blanchard *et al.* (2009), a more generic size-structured model has been described, which simulates the energy flow through the marine ecosystem from phytoplankton to large piscivorous fish.

Probably the most important constraint of zooplankton parameterisation in biogeochemical models is related to the sources of mortality. Since most LTL models do not simulate trophic levels above secondary consumers, this mortality term closes the energy and mass balance of the model and is often used to calibrate the ecosystem model to observations rather than applying realistic mortality rates. This subsequently limits the models ability to resample seasonal and interannual variability in zooplankton dynamics correctly. Furthermore, the fact that the balance between bottom-up and top-down controls is not static and the strengths of each can vary temporally underpins the necessity to incorporate a dynamical formulation for high trophic level (HTL) predation in classical LTL models.

Here, we aim to assess the importance of HTL predation for zooplankton dynamics at different time-scales across a range of regional marine ecosystems in the northern and southern Atlantic Ocean. First, we scrutinize the existing literature with respect to trophic control on zooplankton dynamics, bottom-up and top-down, and how these might structure regional foodwebs. Second, we review how zooplankton mortality is currently parameterized within different modelling approaches. We also discuss the applicability of different model parameterizations for ecosystems with different trophodynamics and provide recommendations for future model developments.

Importance of the top-down control of zooplankton in regional Atlantic ecosystems

The analysis of the trophic control of a specific ecosystem usually requires the concomitant analysis of several datasets (Frank *et al.*, 2006) and/or very specific observations on predator–prey interactions. Nonetheless, information collected from the available literature on trophic interactions indicates the implications for zooplankton dynamics. Here, we emphasize six different, high-productive Atlantic ecosystems (Figure 2) including the Bay of Biscay, North Sea, Baltic Sea, Norwegian Sea, Georges Bank (GB)/Gulf of Maine (GoM), and the southern Benguela upwelling system. The ecosystems were chosen to cover a wide range of possible ecosystem drivers (upwelling, tides, mixing, exchange with the open ocean) and a plurality of climatic conditions. Furthermore, we chose to include an ecosystem with very specific characteristics such as the Baltic Sea (permanent halocline, restricted exchange with the open

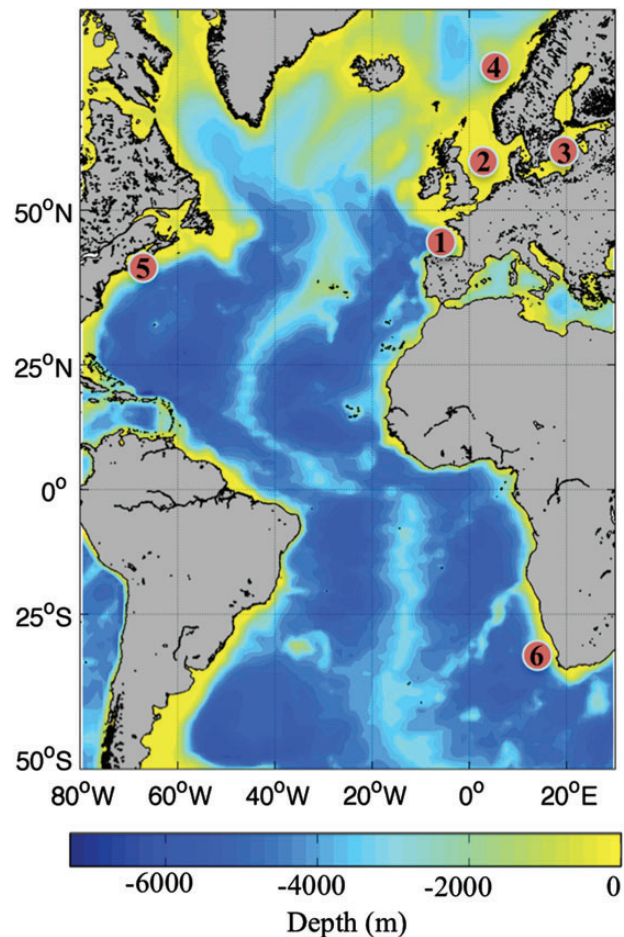


Figure 2. Topography of the Atlantic Ocean and location of the considered regional ecosystems (1, Bay of Biscay; 2, North Sea; 3, Baltic Sea; 4, Norwegian Sea; 5, GB/GoM; 6, Southern Benguela).

ocean) to be compared with open regional ecosystems (North Sea, Bay of Biscay).

Bay of Biscay

The Bay of Biscay is an open oceanic bay in the Northeast Atlantic (NEA) including a continental shelf in the French sector, which is between 150 and 180 km wide in the most northern part (Armorican shelf), becoming narrower, ~50-km width, towards the southern part (Aquitaine shelf) with a minimum extent in the Spanish sector (Cantabrian Sea). The shelf descends rapidly in the abyssal plain more than 4000 m deeper.

The Bay lies in the inter-gyre region that separates the major oceanic gyres of the North Atlantic: the subpolar and the subtropical gyre and as such is part of the Subtropical-Boreal transition zone. This, together with the effects of the general circulation and a variety of local hydrodynamic drivers (plumes, mesoscale eddies, fronts, upwelling), explains the relatively high diversity and variability in time and space of zooplankton species found in the area. Poulet *et al.* (1996) reported from a literature review that about 300 species of zooplankton exist in the system including open-ocean to coastal and neritic species, among which 10% are copepods. The latter account for ~60–95% of the numerical abundance of zooplankton. Over the shelf, copepods constitute the bulk of the zooplankton biomass, whereas meroplankton form the majority of

zooplankton biomass in estuarine habitats (Valdés *et al.*, 2007). The copepod fauna are dominated by smaller species such as *Oncaea media*, *Paracalanus parvus*, *Clausocalanus* spp., *Oithona* spp., *Pseudocalanus elongatus*, and *Temora* spp., as reported from observations over the Spanish shelf (Valdés *et al.*, 2007). In further offshore areas of the bay and at the entrance of the English Channel, *Acartia clausi*, *Calanus helgolandicus*, and *Centropages typicus* also contribute significantly to the zooplankton community (Poulet *et al.*, 1996).

The spatial structure of the Bay of Biscay ecosystem helps explain the large onshore to offshore gradient in species diversity and distribution (Albaina and Irigoien, 2004; Zarauz *et al.*, 2008; Irigoien *et al.*, 2009) as well as abundance and size distribution (Nogueira *et al.*, 2004; Sourisseau and Carlotti, 2006; Irigoien *et al.*, 2009). Habitats include nutrient-rich coastal areas displaying steepest slopes of the zooplankton size spectra, as well as oligotrophic, offshore areas with lower slopes. Locally, in the presence of fronts such as over the shelf edge, this gradient may be disrupted (Albaina and Irigoien, 2004), and shelf waters may enter offshore waters trapped in slope eddies (Fernández *et al.*, 2004).

The main planktivorous species in the Bay of Biscay are clupeids [European sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*), and European sprat (*Sprattus sprattus*)], as well as mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*), and chub mackerel (*Scomber japonicus*). In the latter three species, zooplankton forms a large portion of the diet during a large part of their life cycle. Common sole (*Solea solea*), blue whiting (*Micromesistius poulassou*), European hake (*Merluccius merluccius*), and anglerfish (*Lophius piscatorius* and *Lophius budegassa*) form the majority of the benthic and demersal species feeding on zooplankton only during the early parts of their life cycle.

Based on a literature review and new growth rate estimates, Poulet *et al.* (1996) reported that copepod production is generally food limited in the bay. In a more recent and global effort, Lassalle *et al.* (2011) found evidence from an Ecopath with Ecosim (EwE) modelling analysis that the mid-shelf ecosystem was structured by bottom-up processes, particularly looking at the effect of changes in mesozooplankton on forage fish. However, as the relative importance of bottom-up and top-down mechanisms may depend on the temporal and spatial scale, and because a wide range of different habitats exists from the coast to off-shelf areas, further studies are needed at different temporal and spatial scales to thoroughly characterize the dominant trophodynamic controls.

Generalized Additive Modelling analysis of a 10-year time-series of monthly phyto- and zooplankton abundance revealed that the seasonal dynamics of plankton over the Spanish shelf is primarily driven by abiotic factors suggesting strong bottom-up regulation (Stenseth *et al.*, 2006), which is related to the classical food chain (microphytoplankton direct link to mesozooplankton) along the coast and during the spring bloom (Herbland *et al.*, 1998; Stenseth *et al.*, 2006; Marquis *et al.*, 2011). At the outer shelf and after the spring bloom, the ecosystem dynamics exhibit a more complex structure, where the microbial loop takes over and mesozooplankton grazes mostly on microzooplankton (Sautour *et al.*, 2000; Stenseth *et al.*, 2006; Marquis *et al.*, 2007). Still, in this situation, there is no indication for a significant impact of top-down processes on the zooplankton dynamics (Stenseth *et al.*, 2006). Based on an inverse analysis approach of biomass and production data collected in northern areas of the Bay of Biscay, Marquis *et al.* (2011) estimated that the potential export of carbon from plankton to small pelagic fish depends on the structure of the planktonic

foodweb. During the microphytoplankton spring bloom, the carrying capacity is high but the trophic efficiency is relatively low due to high sedimentation export to the benthic community. In more oligotrophic areas of the bay or during the post-bloom periods, the carrying capacity is lower but the trophic efficiency is higher, with a tighter coupling between primary production and small pelagic fish in a microbial foodweb environment. Under this situation, predation by planktivorous fish may potentially exert local top-down control on mesozooplankton (Dupuy *et al.*, 2011; Marquis *et al.*, 2011).

The complex spatial and temporal structuring of zooplankton communities described in the Bay of Biscay linked to the system dynamics makes it challenging to assess the relative roles of bottom-up and top-down processes affecting the zooplankton. However, most of the aforementioned studies indicate that bottom-up processes basically structure the zooplankton in the Bay of Biscay.

North Sea

The North Sea is a highly dynamic shelf sea ecosystem with major opening to the North Atlantic and a pronounced frontal system that consists of both tidal and salinity fronts, which are located primarily in the southern North Sea (Dogger Bank and the German Bight) and along the Norwegian Trench. The frontal system forms a transition zone between the well-mixed, highly productive areas along the coast and the seasonally stratified central and northern North Sea. Based on the CPR (Continuous Plankton Recorder) phytoplankton colour index, Edwards *et al.* (2002) described multi-decadal changes in phytoplankton biomass. After a minimum in the late 70's, phytoplankton biomass increased rapidly until the late 80's when it reaches a persistent higher biomass when compared with the previous decades.

The ecosystem exhibits high species diversity in both zooplankton and fish. Extensive reviews of the resident zooplankton and fish assemblage have been previously published by a number of authors (Daan *et al.*, 1990; Fransz *et al.*, 1991). A number of studies report that copepods form the dominant zooplankton in the North Sea, although in March and April, euphausiids were found to represent 90% of the total zooplankton biomass (Williams and Lindley, 1992). In general, >26 zooplankton taxa have been reported to occur in the North Sea and NA Ocean (Colebrook *et al.*, 1984) but a number of studies (Fransz *et al.*, 1991) indicates a clear dominance of the *Pseudocalanus* sp. and *C. finmarchicus*. Additionally, *T. longicornis*, *Acartia* spp., *C. typicus*, and *P. parvus* have been found to be dominant members of the copepod community. Reviews of the North Sea zooplankton community (Fransz *et al.*, 1991; Krause *et al.*, 1995; Beaugrand *et al.*, 2001) highlight the large diversity of the community and the importance of temperature, latitude, and/or season in terms of species composition and abundance.

Over 200 fish species have been identified in the North Sea that can be partitioned into seven groups of species with major biomass contributions from demersal gadoids, flatfish, clupeids and sandeels (*Ammodytes marinus*; Daan *et al.*, 1990). The larval stages of the vast majority of species rely on copepods as a principle diet item. Although large gadoids such as Atlantic cod (*Gadus morhua*) switch to piscivory as large juveniles or adults, smaller-bodied species such as Norway pout (*Trisopterus esmarkii*) and various clupeids, such as herring (*Clupea harengus*) and sprat, and sandeel remain planktivorous throughout their whole life. Zooplankton consumption by fish has been estimated by Heath (2007) to be 19–25 g C m⁻² year⁻¹ of which ~28% of the overall zooplankton consumption by fish can be assigned to early life

stages (larvae and juveniles). Munk and Nielsen (1994) sampled the larval fish and zooplankton community at Dogger Bank in autumn 1991 and reported little potential for the top-down control of zooplankton by ichthyoplankton in many regions except at frontal zones where larvae could consume up to 3–4% day⁻¹ of the fraction of preferred zooplankton size classes. This level of feeding was in the same order of magnitude as zooplankton production during that study period (late spring and summer) and it was expected that zooplankton biomass in frontal areas could be depleted due to feeding by other zooplanktivores (juvenile and adult fish, gelatinous plankton, etc.). Working in the same region earlier in spring, Nielsen and Munk (1998) found little evidence for impacts of larval fish predation on the zooplankton community. Seasonal variability in the potential for (local) top-down control is not unexpected given the more rapid rates of zooplankton production, colder water temperatures, and relatively low abundance of young-of-the-year fish during spring compared with summer. In autumn, the combination of lower rates of zooplankton production, warmer water temperatures, and the higher abundance of young-of-the-year fish makes the local depletions of zooplankton by predatory more likely.

The North Sea has exhibited shifts in fish species composition (e.g. Heath, 2005; Dulvy et al., 2008) that are expected to alter the relative strength of top-down vs. bottom-up processes affecting zooplankton. Similarly, the zooplankton species composition of the system changes both spatially and temporally in response to changes in environmental factors (e.g. Krause et al., 1995; Edwards et al., 2010; Lindley and Batten, 2010). A number of observational studies has reported a general decline in the abundance of key species of zooplankton (Colebrook et al., 1984; Pitois and Fox, 2006) accompanied by a shift towards smaller copepods after 1980 reflecting a large-scale regime shift of the North Sea towards an equilibrium characterized by warmer-water species (Beaugrand and Reid, 2003; Pitois and Fox, 2006).

Hence, the magnitude of zooplanktivory by fish and other predators and the potential role of top-down vs. bottom-up processes cannot be considered constant, making it challenging to assess the ecological state of the system. Nonetheless, Heath (2005) reported that the pelagic foodweb of the North Sea was, in general, bottom-up controlled at least between 1973 and 2000 despite the changing hydrographical and ecological conditions in the 1980's.

Baltic Sea

The Baltic Sea is a brackish mediterranean sea with a small and shallow opening to the North Sea and high inputs of freshwater and nutrients from the catchment area generating a permanent halocline. In general, the Baltic Sea can be separated into two different ecosystems, the transition zone between Baltic Sea and North Sea including the Skagerrak, the Kattegat, the Danish straits and Fehmarn Belt, and the Baltic Sea Proper. The transition zone is characterized by a steep salinity gradient ranging from 32 in the Skagerrak to around 9 in the Fehmarn Belt. In the central and eastern part of the Baltic Sea surface, salinities vary from 8 to 2 (Maar et al., 2011). Water exchange between the Baltic Proper and the North Sea is strongly limited by the narrow straits and locally very shallow topography enabling Major Baltic Inflows from the North Sea to occasionally occur under specific atmospheric conditions (Gustafsson, 1997).

Transition zone

Primary production in the transition zone follows a clear seasonal pattern with very low production rates from November to February

(Rydberg et al., 2006) and two production maxima. The spring bloom initiates the productive season in March to April followed by a second peak in late summer between July and September. The average annual primary production is relatively high with around 100–200 g C m⁻² year⁻¹ in open waters and up to 500 g C m⁻² year⁻¹ in coastal regions (Rydberg et al., 2006).

The dominant copepod species in terms of biomass are *P. minutus* and *Centropages* spp. (Zervoudaki et al., 2009) followed by *T. longicornis*, *P. elongatus*, *P. parvus*, *Acartia* spp., *Oithona* spp., *C. helgolandicus*, and *C. finmarchicus* (Kjørboe and Nielsen, 1994; Maar et al., 2004; Lindegren et al., 2010). The copepod biomass varies seasonally following a unimodal pattern with maximum values between midsummer and autumn (Zervoudaki et al., 2009).

Important predators of zooplankton are carnivorous copepods, chaetognaths, jellyfish, and fish (Tönnesson and Tiselius, 2005; Tönnesson et al., 2006; Dinasquet et al., 2012). Since the transition area is relatively shallow, benthic filter-feeders (e.g. bivalves) are important predators that can exert the control of the biomass of copepods in addition to the pelagic predators (Maar et al., 2007; Nielsen and Maar, 2007; Tiselius et al., 2008). The biomass of predators of zooplankton is generally highest from late summer to autumn (Tönnesson and Tiselius, 2005; Tönnesson et al., 2006) causing highest copepod predation mortality in this period. Generally, copepod seasonal mortality in the Kattegat was estimated to 3.0–15.0% day⁻¹ (Kjørboe and Nielsen, 1994). Copepod egg mortality was highest during the spring bloom, probably due to cannibalism and low hatching success as shown in Kjørboe and Nielsen (1994). Those authors concluded that the seasonal development of copepods depended on both productivity and mortality, but that mortality was the most important factor shaping the temporal dynamics of copepod abundance after the spring phytoplankton bloom. Although time-series of zooplankton biomass in offshore waters since 1989 suggest no temporal trends (Hansen and Petersen, 2011), Lindegren et al. (2010) analysed a longer time-series of zooplankton capture in Oresund (Danish Straits) and reported a significant decrease in zooplankton biomass after 1988/1989. The abundance of *Pseudocalanus* spp. has displayed a particularly strong response (decrease) to salinity changes (freshening) and was also positively correlated with landings of herring and cod. This suggests that the system is mainly bottom-up controlled in the Oresund (Lindegren et al., 2010). In the Kattegat, however, previous studies imply a seasonal shift from bottom-up control during the spring phytoplankton bloom to top-down control thereafter.

Central Baltic Sea

The Baltic Sea Proper or the open central Baltic Sea (CBS) is a well-studied ecosystem that suffers from eutrophication effects and is subject to intensive fisheries. Here, the zooplankton species composition is primarily limited by low salinities, and the biodiversity is lower than that in the transition zone. The dominant zooplankton groups, in terms of biomass, are copepods including *P. acuspes*, *T. longicornis*, *Acartia* spp., and *C. hamatus*. In addition, cladocerans are abundant during summer (Möllmann et al., 2000; Schulz et al., 2012). The CBS zooplankton community is vertically structured by the permanent halocline. For example, *Acartia* spp. and *T. longicornis* inhabit the fresher waters in the surface layer (0–30 m), whereas *P. acuspes* is mainly found in the halocline region, which separates the surface water from the more saline bottom water at around 70-m depth (Hansen, 2005; Schulz et al., 2012). The vertical structure also affects the potential overlap between

zooplankton species and their predators. The main fish species preying on open sea zooplankton are the clupeids sprat and herring for which copepods form the major food source (Arrhenius and Hansson, 1993).

Phytoplankton production has a very distinct seasonal pattern in the CBS, where peak production occurs between March and May, followed by a more modest, but longer lasting production during summer (June–August). Diatoms and flagellates are most important during spring and fall but summer production is fuelled by nitrogen fixing cyanobacteria. At the time of the spring bloom, cold water temperatures limit zooplankton production and the highest zooplankton abundances are observed directly after the late-summer production maximum between July and September (Möllmann *et al.*, 2000). During winter, the zooplankton abundance is at a minimum and comparable with what is observed in the transition zone. During the last decades, the phytoplankton biomass and compositions was observed to undergo major changes particularly in spring. Wasmund *et al.* (1998) reported a sudden increase in spring primary production constituted by an increase in dinoflagellates but a decrease in diatoms. Production of mesozooplankton in spring was basically following this pattern with a major increase in the biomass of *T. longicornis* and *Acartia* spp. at the end of the 1980s (Alheit *et al.*, 2005) and has been found to be dominantly impacted by environmental forcing (Möllmann *et al.*, 2000).

In contrast, the predation impact of clupeids on different stages of copepods was found to be relatively low. Möllmann and Köster (2002) estimated the average consumption per production (fish consumption/copepod gross production at a developmental stage) ratio being much below 0.1 between 1977 and 1996, using net samples for copepods and stomach samples of the relevant fish species. However, at times, clupeid fish were found to consume major proportions (up to total potential production) of certain groups of copepod life stages (Möllmann and Köster, 2002), determined by the predator life cycles. For example, herring predation on open sea zooplankton (*P. acuspes* and *T. longicornis*) is relatively low during the spawning season spring-spawning herring, when herring inhabits the coastal areas, in contrary to the summer and winter situation. Sprat, in contrast, exerts major predation pressure on certain stages of *P. acuspes* and *T. longicornis* particularly during spring. In addition, zooplankton is assumed to form more than half of the autumn diet of mysids (Viherluoto *et al.*, 2000), although only limited information is available about mysid abundance and the importance of their role in the CBS ecosystem.

During the past decades, a decrease in the *P. acuspes* abundance has been observed, whereas *Acartia* spp. and *T. longicornis* have increased (Möllmann *et al.*, 2000). These changes could partly be explained by climate-driven changes in temperature (warming) and salinity (freshening). However, also large changes in trophic control were observed, particularly in relation to the late 1980s CBS regime shift, when the ecosystem switched from a cod to a sprat-dominated state (Casini *et al.*, 2008; Möllmann *et al.*, 2008). Increased predation by sprat resulted in a clear biomass decrease in *P. acuspes*, which is a preferred prey of both sprat and juvenile cod. Furthermore, analyses by Casini *et al.* (2009) suggested that the abundance of *P. acuspes*, which was primarily related to changes in salinity before the regime shift, was correlated with sprat biomass (indicating top-down control) after a threshold for sprat abundance was exceeded. At the ecosystem level, sprat predation on *P. acuspes* may also be a mechanism that stabilizes the sprat-dominated state, since large numbers of sprat may outcompete

juvenile cod for prey resources, hindering growth of the cod stock (Möllmann *et al.*, 2009).

Taken together, the existing studies indicate that both bottom-up/environmental and top-down/predation processes can control all or parts of the Baltic Sea zooplankton community. Nonetheless, the relative importance of these processes is variable on both seasonal and interannual time-scales. Moreover, Casini *et al.* (2008) proposed that changes within CBS higher trophic levels may not only affect the level of secondary production, but also might cascade down to primary producers, indicating a tightly interlinked foodweb.

Norwegian Sea

The Norwegian Sea comprises a continental shelf, a steep continental slope and ocean basins with depth of more than 3000 m. The ocean climate is dominated by warm, saline Atlantic water penetrating northwards along the Norwegian coast and colder Arctic water masses in the eastern parts and beneath the Atlantic water. In general, the area is characterized by extensive frontal activities and mesoscale eddies, which are important for marine ecosystem dynamics, as exemplified in observational study by Godø *et al.* (2012) and in modelling experiments by Samuelsen *et al.* (2012). The herbivorous copepod *C. finmarchicus* (Gunnerus) is the dominant mesozooplankton species in the Norwegian Sea and thus the dominant link between primary production and higher trophic levels (Aksnes and Blindheim, 1996; Melle *et al.*, 2004). *C. finmarchicus* follows a seasonal vertical migration cycles, remaining in diapause at depths of ~500–1500 m during winter, ascending to surface waters in spring to feed on the phytoplankton spring bloom, and descending back to deeper water layers in late summer. Main predators for *C. finmarchicus* are herring and carnivore zooplankton species such as amphipods, medusae, and krill, but the role of *C. finmarchicus* in the ecosystem is complex due to branching and interconnections in the foodwebs (Gislason and Astthorsson, 2002; Melle *et al.*, 2004). Recent observations indicate that zooplankton abundance in the Norwegian Sea has declined from 18 to 6 g m⁻² between 2002 and 2011 (Huse *et al.*, 2012a).

Diatoms form the major phytoplankton group in the Norwegian Sea followed by flagellates (Rey, 2004). Annual open ocean primary production is estimated from various sources of survey data at ~80 g C m⁻² (Rey, 2004), with very low phytoplankton production in winter followed by a strong spring phytoplankton bloom and a weaker late summer/autumn bloom. Interannual variability in the primary production of the Norwegian Sea is relatively small (Mueter *et al.*, 2009), due to limited variability in late-winter nutrient concentrations and a consistent pattern of production (Rey, 2004). The cycles of primary and secondary production of the Norwegian Sea are tightly coupled with a high rate of energy transfer to higher trophic levels.

The Norwegian Sea forms the feeding ground for some of the largest, commercially exploited fish stocks in the world and the fish community in the Norwegian Sea underwent notable changes during the last decades. The biomass of the “pelagic complex” in the Norwegian Sea [Norwegian spring-spawning herring, blue whiting, and the NA mackerel] has steadily increased and reached 15 million tonnes in 2004, remaining fairly high until 2010 (Huse *et al.*, 2012a). Over the course of the same period, these planktivorous fish changed their migration pattern resulting in a more westward distribution of these species (Utne *et al.*, 2012b, based on survey data). Additionally, signs of intra- and interspecific competition were observed within the pelagic complex, as well as negative relationships

between length-at-age and stock biomass (Huse *et al.*, 2012b). Results from the fully coupled physical–biological modelling system norwecom.e2e (Hjøllo *et al.*, 2012) also suggest that planktivorous stocks exert a considerable predation pressure on the zooplankton resource (Utne and Huse, 2012), but the ecological impacts of high abundance of planktivorous fish on zooplankton are complex. For example, high abundances of planktivorous fish could indirectly reduce predation pressure on *C. finmarchicus*, since planktivorous fish also feed on krill, amphipods, and mesopelagic fish, which are known predators for *C. finmarchicus*.

Bottom-up control of the Norwegian Sea ecosystem has been documented from various sources of observations, with climate variability directly driving variability in the recruitment of some of these fish stocks by impacting the spatial extent and distribution of nursery areas, but changes in zooplankton biomass have also been related to changes in upper trophic levels (Skjoldal and Sætre, 2004). Mueter *et al.* (2009) reported a negative correlation between inter-annual changes in zooplankton biomass in the Norwegian Sea and its dominant predator herring, and Huse *et al.* (2012a) stated that the high biomass of planktivorous fish in the Norwegian Sea led to depletion of their common prey resource, indicating the possibility of top-down control on zooplankton dynamics in the system. Thus, it appears likely that top-down processes determine interannual variability in zooplankton biomass.

Georges Bank/GoM

Copepods are the most abundant mesozooplankton in the NW Atlantic Ocean and play a central role in marine foodwebs (Davis, 1987; GLOBEC, 1992; Mitra and Davis, 2010). In the GoM and GB region, the dominant copepod species are *C. finmarchicus*, *Pseudocalanus* spp., *O. similis*, *Centropages* spp., *T. longicornis*, *Metridia* spp. (primarily *M. lucens*), and *P. parvus* (Bigelow, 1924; Davis, 1984, 1987; Sherman *et al.*, 1987; Durbin *et al.*, 2003; Durbin and Casas, 2006). Each species exhibits a characteristic life cycle and seasonal/spatial pattern in the GoM/GB region. *C. finmarchicus*, *M. lucens*, and *Pseudocalanus* spp. are cold-water species that avoid the warm surface layer (>10–12°C) during summer and fall and produce large spring populations. *Centropages* spp., *T. longicornis*, and *P. parvus* are warm-water species and are most abundant during late summer and fall, whereas *O. similis* is plentiful throughout the GB/GoM region year round.

Long-term survey data suggest a strong decadal-scale shift of copepod community structure in the NW Atlantic. For instance, the multidimensional scaling analysis of NEFSC MARMAP/EcoMon [NOAA Northeast Fisheries Service Center (NEFSC) survey includes: MARMAP (Marine Monitoring Assessment and Prediction, 1977–1987) and the subsequent EcoMon (Ecosystem Monitoring, 1988–present) programs] data showed a concomitant decadal shift in the copepod community, with a higher abundance of small species in the 1990s compared with the 1980s and 2000s (Kane, 2007; Hare and Kane, 2012). This decadal shift of copepod community structure also was seen in the CPR data in the GoM region (Greene and Pershing, 2007) and also along the entire NW Atlantic shelf from Newfoundland to the Middle-Atlantic Bight (Pershing *et al.*, 2010). The increase in small-bodied copepods from the 1980s to the 1990s also has been associated with increased haddock (*Melanogrammus aeglefinus*) recruitment and with a system-wide change in the fish community of the NW Atlantic shelf and the fisheries associated with them (Link *et al.*, 2002; Mountain and Kane, 2010). The decadal variability in individual,

small copepod species such as *C. typicus* and *Pseudocalanus* spp. is also in line with the overall pattern: high in the 1990s but low in the 1980s and 2000s (Ji *et al.*, 2012b).

The exact causes of the observed variability are difficult to determine, but likely involve the combination of both bottom-up and top-down controls. It has been hypothesized that climate forcing could have impacted the copepod populations in the NW Atlantic through bottom-up processes, mainly involving changes in surface salinity and water column stability and the resulting changes in fall-winter phytoplankton blooms (e.g. Durbin *et al.*, 2003; Durbin and Casas, 2006; Greene and Pershing, 2007; MERCINA Working Group, 2012). This salinity–zooplankton relationship is significant for the years during the 1980s and 1990s, but starts to break down during the 2000s, when lower salinity is not associated with higher abundance of small zooplankton (Hare and Kane, 2012). Top-down control has also been considered as a possible cause of variation in zooplankton abundance. Frank *et al.* (2005, 2011) proposed a trophic cascade hypothesis in the Nova Scotian Shelf region (upstream of the GoM) based on the regression analyses of fish and plankton time-series. This hypothesis is supported by the fact that overfishing of large-bodied demersal fish (and their subsequent population collapses) resulted in the dominance of planktivorous forage fish, which reduced the abundance of larger (≥ 2 mm) zooplankton in the region. The smaller (<2 mm) zooplankton, however, increased with the increase in forage fish. Such a trophic cascade is less evident in the GoM region (Frank *et al.*, 2006). Ji *et al.* (2012b) used a coupled hydrodynamics/foodweb/population dynamics model (based on earlier work by Ji *et al.*, 2009; Stegert *et al.*, 2012) to assess the sensitivity of the *Pseudocalanus* spp. and *C. typicus* to changes in phytoplankton biomass and bloom timing, as well as the changes in the mortality regime. The results showed that the modelled species are more sensitive to changes in mortality rates than to food availability and peak timing. Bottom-up processes alone cannot explain the observed variability in *Pseudocalanus* and *Centropages* population sizes, whereas top-down controls play a critical role in copepod population dynamics in the GoM region. It is worth noting that the top-down control of zooplankton populations are not only driven by fish populations, but more important by invertebrates such as chaetognaths, hyperiids, and gelatinous zooplankton, which are often difficult to quantify (e.g. Davis, 1984; Ji *et al.*, 2012b).

Southern Benguela

The Benguela current is located along the southwest coast of Africa and characterized by near coastal upwelling. Based on differences in upwelling characteristics and hydrographic conditions (Rae, 2005), the Benguela is often divided into two subsystems north and south of the Lüderitz upwelling cell. In contrast to the northern part at the Namibian coast with permanent upwelling, the southern part along the South African coast is characterized by seasonally variable upwelling with a maximum observed from September to March (Shannon, 1985). The southern Benguela differs generally from other upwelling systems by the presence of the warm Agulhas Current on the south coast of South Africa, which follows the continental shelf on the east part of the Agulhas Bank. Thereby, it extends further offshore as the continental shelf broadens (until its maximum of 230 km in Cape Infanta), before going backwards (retroflexion) and simultaneously creating the Agulhas rings (Gordon and Haxby, 1990), large eddy structures that allow a transport of warm water into the South Atlantic Ocean. At the junction of the two oceans, a jet occurs along the 200–300-m isobaths at the

narrowest point of the continental shelf (in front of Cape Town). This jet is very important from a biological point of view as it allows the passive transport of fish eggs and larvae from the spawning ground (Agulhas Bank) to the nursery areas in west.

Upwelling areas constitute highly productive systems due to nutrient-rich waters upwelled leading to high phytoplankton production. Phytoplankton is dominated by diatoms, which have high nutrient requirements and are well adapted to turbulent conditions. Nevertheless, small phytoplankton cells (flagellates) might dominate nearshore waters. From a bottom-up perspective, high primary production should support high fish biomass. However, compared with other marine systems, productivity at the base of the foodweb is not efficiently converted into fish production (Jarre-Teichmann *et al.*, 1998). Zooplankton may play a critical role in the transfer efficiency (or rather inefficiency for upwelling systems) between primary production and fish production (Hutchings, 1992). This ecosystem is characterized by a large abundance of zooplankton but rather low species diversity mainly due to its cold waters compared with the adjacent Agulhas Current. The main taxa living in the cold waters of the Benguela current are *C. brachiatus*, *C. carinatus*, *M. lucens*, *N. minor*, *C. arcuicornis*, *P. parvus*, *P. crassirostris*, and *C. vanus*.

In the southern Benguela upwelling system, planktonic crustaceans have increased by more than 1 order of magnitude between 1951 and 1996 (Verheye and Richardson, 1998; Verheye *et al.*, 1998). Hutchings *et al.* (1995) showed that the main factor controlling copepod production was the variation in biomass and demographic structure, inversely correlated with fish density but also associated with hydrographical conditions. Corroborating the existence of a bottom-up control, the long-term increase in zooplankton is linked to an increase in the upwelling favourable wind (Verheye and Richardson, 1998). The latter can induce (i) an increase in phytoplankton biomass due to enrichment of nutrients, (ii) advections of planktonic populations from upwelling cells further south in the region, and (iii) alterations of the current field of semi-closed areas. These mechanisms, combined with the vertical migration ability of zooplankton, may increase its retention in coastal areas (Verheye, 2000). On the contrary, when comparing zooplankton increase with fish trends, top-down control seems to operate in the Benguela upwelling. This ecosystem supports a large population of small pelagic fish composed of anchovy and sardine, which display a decrease in total biomass since the 1950s, thus resulting in a long-term reduction in the predation pressure on zooplankton. Furthermore, anchovy and sardine populations have shown alternations in abundance, which can be linked to the size structure of zooplankton community (Verheye and Richardson, 1998; Verheye *et al.*, 1998). Whereas sardine is known to feed on small zooplankton (Van der Lingen *et al.*, 2002), anchovy rather target large zooplankton (Van der Lingen *et al.*, 2006). The shift from sardine (*S. pilchardus*) dominance (1951–1967) to anchovy dominance (1988–1996) coincided with an increase in small crustaceans (<0.9 mm) and a decrease in larger ones (Verheye and Richardson, 1998).

These studies derived from observations lead to the conclusions that both bottom-up and top-down mechanisms operate in concert rather than alone in the Benguela ecosystem. Top-down control from small pelagic fish affects both the abundance and size structure of zooplankton. Upwelling ecosystems have been characterized as “wasp-waist” (Cury *et al.*, 2000) as small pelagic fish exert bottom-up control on top predators and top-down control on zooplankton that potentially cascade down to phytoplankton. Under this “wasp-

waist” control hypothesis, zooplankton is highly vulnerable to predation by small pelagic fish.

Zooplankton mortality in LTL and coupled ecosystem models

The majority of models emphasize specific parts of the food chain and, therefore, risk neglecting important dynamical processes related to feedback mechanisms with other trophic levels. A large part of available marine ecosystem models can be differentiated into LTL NPZ(D) models [so called NPZ(D) models or LTL models; e.g. Moll and Radach, 2003; Skogen *et al.*, 2004; Schrum *et al.*, 2006; Huret *et al.*, 2013] and higher trophic level models (HTL models) that represent mainly fish at different developmental stages, such as single-species IBMs (e.g. Megrey *et al.*, 2007; Vikebø *et al.*, 2007; Daewel *et al.*, 2008a; Peck and Hufnagl, 2012) or multi-species models such as OSMOSE (Shin and Cury, 2001, 2004). Although in some models, such as EwE (Christensen and Pauly, 1992), norwecom.e2e (Hjøllo *et al.*, 2012; Utne *et al.*, 2012a), or Atlantis (Fulton *et al.*, 2003; Fulton, 2010), more trophic levels are included, other approaches utilize offline coupling between LTL and HTL models when aiming to link the trophic levels, which assumes bottom-up control in the system. This lack of a dynamical link between LTLs and higher trophic levels has important implications for the simulated zooplankton dynamics and limits the ability of both types of models to adequately simulate spatial and temporal changes in ecosystem dynamics. In the following, we review the available modelling approaches with respect to their ability to simulate zooplankton mortality adequately (Figure 1), which is necessary for modelling the energy transfer from LTL to fish.

Zooplankton mortality in LTL models

Fixed mortality rates

The vast majority of NPZ models are “closed” by using a relatively simple fixed formulation for zooplankton mortality (μ), which usually does not disentangle different sources of mortality. This closure term is defined as $\mu = \gamma(d, Z)$ and depends on the constant mortality rate d and the zooplankton biomass Z , where $\gamma(d, Z)$ can be defined in different functionalities that either allow consideration of density-dependent mortality or not. Edwards and Yool (2000), motivated by the earlier work of Steele and Henderson (1992), tested the impact of the four different functional forms of the closure term (linear, quadratic, hyperbolic, and sigmoidal) in each of two different models (a simple NPZ model and a more complex seven-component NPZ model). Their results indicate that the steady state solution of the simple model can be very sensitive to the choice of the functional form of the closure term, whereas in contrast more complex models produce more stable solutions with rather similar results for all closure terms. The authors specifically assessed the appearance of limit cycles with respect to the choice of the closure term and found those to occur in three of the four cases, but with highest likelihood for the linear closure term. The maximum of those short-term oscillations can be well above the steady state solution and has also a quantitative effect on the model results. The appearance of limit cycles is only one general constraint of the approach among others. First, the parameters are difficult to define and the parameterization is usually not empirically motivated. Second, the spatial-temporal dynamics of predator abundances is not included in the approach thus seasonal dynamics and small-scale variability in zooplankton predation mortality cannot be covered by this general approach. This is a

clear disadvantage, since our review on predation impacts on zooplankton dynamics in different marine ecosystems as well as findings by several other authors (Ohman *et al.*, 2004; Travers *et al.*, 2007; Ohman and Hsieh, 2008; Neuheimer *et al.*, 2009; Plourde *et al.*, 2009) highlight the necessity to account for spatial-temporal differences in predator abundance to estimate ecosystem functionalities.

Mortality rates from observations

One solution to make zooplankton mortality terms more dynamic and realistic could be to apply spatially explicit estimates of mortality rates from observation as in the uncoupled formulation of the European Regional Sea Ecosystem Model (ERSEM; Bryant *et al.*, 1995). In that case, consumption rates and biomasses of potential predators were used to estimate zooplankton mortality rates (due to predation) within each of the ERSEM boxes in the North Sea. This approach requires a lot of data and knowledge of predator consumption rates, provides mortality rates strongly biased by the available observations, and concentrates on the predatory mortality only. In contrast, accumulated zooplankton mortality rates can be derived from observed zooplankton population dynamics. As opposed to the horizontal life table (HLT), which follows a group of individuals from birth throughout their life and calculated mortality estimates based on decreases in the abundance of successive life stages, the vertical life table (VLT) approach utilizes data from all life stages collected at one point in time with the advantage that data are easier to collect and advective losses affecting local zooplankton production are accounted for. Aksnes and Ohman (1996) described the method in detail and its potentially drawbacks including the assumptions that successive stages are sampled in an unbiased manner and that transport processes are relatively constant over the duration of at least two life stages. The latter assumption might be unrealistic in highly dynamic systems where populations exhibit continuous breeding characterized by overlapping generations.

From a modelling point of view, the application of observed mortality rates has some additional limitations. *In situ* observations can often not distinguish losses due to different processes and the estimate will either include only one mortality term such as when predator fields are sampled, two terms (natural and predation mortality) as in the HLT approach, or all “loss” terms, including advection, as in the VLT approach. For a three-dimensional interlinked biological–physical LTL model that already considers advection, mortality estimates from the HLT are more suitable than those from the VLT approach. Furthermore, the estimates are usually based on species-specific observations rather than functional groups and, hence, are best applied to species-specific population models or to bulk zooplankton models portraying systems with low zooplankton species diversity (such as the Baltic Sea): it is difficult to scale up these species-specific estimates to zooplankton functional groups. Another limitation occurs when attempting to simulate the long-term changes of an ecosystem and/or making future projections. Since the mortality rates are estimated from “snap shots” of *in situ* conditions, applying them within long-term simulations where ecosystem dynamics and zooplankton characteristics may have changed (e.g. changes in predator composition and biomass, temperature adaptation, or changes in the species composition) is unwise. Despite the limitation related to the methods and to the data coverage, the use of observed mortality rates can be very useful to simulate the general spatial-temporal patterns in the zooplankton community within a system. Furthermore, *in situ* observations can provide important insights in terms of understanding the

interaction between top-down and bottom-up processes by allowing coarse estimates to be made of the zooplankton mortality in the system.

Mortality in size-structured models

In size-structured models such as the ones proposed by Maury *et al.* (2007) and Baird and Suthers (2007), zooplankton mortality including predation is implicitly parameterized when size classes larger than zooplankton are included (sizes of planktivorous fish and larger organisms). A “feeding kernel” is used to account for grazing loss (on the prey side) and energy intake (on the predator side) (Zhou *et al.*, 2010). The “feeding kernel” is parameterized as a mechanistic relationship between predator and prey size and, in general, described by the predation loss μ_p for weight (size) z_1 at time t as:

$$\mu_p(z_1, t) = \int_{z_1}^{z_{\max}} p(z_1, z', t) B(z', t) dz,$$

where $B(z', t)$ is the biomass in the predator size group z' and p the predation rate in the size group z_1 by some other size group z' . The predation rate depends in general on the size of the predator (via swimming speed) and prey density (biomass) which can be expressed using a standard functional response (Maury *et al.*, 2007) or a mechanistic formulation for encounter rates (Baird and Suthers, 2007). The approach provides a consistent formulation for energy flow in the marine foodweb and avoids separating the foodweb into finite trophic levels, which also implies a “closed” zooplankton formulation. Nonetheless, if the model is formulated only for a restricted size range, it still requires an additional closure term such as a quadratic loss term (Baird and Suthers, 2007). A sensitivity study revealed that the model results were highly sensitive to the choice of the upper size limit. Furthermore, the mechanistic formulation of the predation term requires knowledge of a number of parameters such as assimilation efficiency, preferred size range and swimming speed of the predator. Baird and Suthers (2007) noted that disregarding species diversity and related physiological differences among species constrains the applicability of the model. The lack of representation of mechanisms (behaviour, physiology) of members of higher trophic levels also limits the ability of generic size-spectrum models to represent small-scale (spatial and temporal) variability in HTL dynamics (e.g. physiological-based migration strategies).

To avoid the parameterization problems, Zhou *et al.* (2010) applied a scale analysis to simplify the formulation for the net abundance change due to mortality μ in a size class z_1 at time t to a function of growth rate g and the mean (averaged over the integration period) slope of the biomass spectra S [their Equation (24)] such that $\mu(z_1, t) = gS$. This approximation not only helps to avoid a complex parameterization, but it also addresses the closure problem, since it does not require additional information from larger size classes. Although the aforementioned models were designed to cover “all” trophic levels with a consistent size spectrum theory, the approach proposed by Zhou *et al.* (2010) emphasizes particularly the closure problem of NPZ-type LTL models. Their “size spectrum zooplankton closure model” (Zhou *et al.*, 2010) simulates zooplankton dynamics based on relevant biological processes including individual growth, population mortality, and biomass energy fluxes. The model is driven by phytoplankton biomass, temperature, and the mean slope of the biomass spectrum why it is highly applicable to be coupled to LTL primary production models. The model has been

tested against observations using observed phytoplankton biomass to force the model (Zhou *et al.*, 2010) and was found to be reasonably good in estimating the seasonal variability in both zooplankton biomass and biomass spectra but overestimated zooplankton by a factor of 10, which can probably be assigned to uncertainties in both the model parameterization and field observations. This closure model has a high potential to adequately simulate seasonal changes in zooplankton dynamics and is particularly useful when coupling to HTL IBMs, which often require size-resolved zooplankton fields as input (Lough *et al.*, 2006; Daewel *et al.*, 2011). But, when the model is coupled to a three-dimensional LTL model, some constraints need to be considered. First, as described by Zhou *et al.* (2010), solving the model equation with an upwind finite difference scheme (applied in many LTL models), restricts the time-step due to the Courant–Friedrich–Lewy condition (Courant *et al.*, 1928). Second, the mean slope of the biomass spectrum for the simulation period must be known (e.g. from observation). Deriving mortality rates based on the mean slope of the size spectrum makes this model highly applicable for examining specific dynamics of regional ecosystems but small-scale spatial-temporal variability in predator abundance and predation rates are not resolved. Third, in a three-dimensional ecosystem model, zooplankton biomass and the biomass spectrum is likely to change due to the advection of plankton.

Zooplankton mortality in coupled LTL–HTL modelling approaches

To solve the closure term problem and allow the energy transfer from lower to higher trophic levels to be more realistically simulated [to allow “end-to-end” (E2E) modelling], HTL modelling tools can be coupled to biogeochemical models. An overview of the advances in E2E models has been given by Travers *et al.* (2007). In the following, we will focus on the implementation of a zooplankton closure term in these linked LTL–HTL models. One of the major constraints here is the original role of the closure term as a calibration parameter for the LTL ecosystem models, which needs to be accounted for when additional dynamical predation rates are considered.

Single-species HTL models

One possibility to dynamically couple LTL to HTL ecosystem models is to include a population model for a single fish species (Bryant *et al.*, 1995; Megrey *et al.*, 2007; Oguz *et al.*, 2008). This kind of model mostly emphasizes the fish population rather than zooplankton dynamics. Nonetheless, fish and zooplankton are solved simultaneously creating a dynamical link between the two and allowing for spatial-temporal estimates of predation on zooplankton at least resolving the impacts of one targeted planktivorous fish species on zooplankton. For example, an age-structured population model for Atlantic herring was coupled to the LTL ecosystem model ERSEM (Bryant *et al.*, 1995), whereas a similar model for Pacific herring (*Clupea pallasii*) was coupled to the LTL model NEMURO (Megrey *et al.*, 2007). In both examples, predator–prey interaction was parameterized using a standard Holling type II functional response (Holling, 1959). Although the approach gives a good example of how a population model can be applied to deduce the dynamical estimates of zooplankton mortality, it still does not allow a quantitative estimate of the latter since predation by the remaining planktivores (including larval fish, gelatinous plankton, etc.) is still represented by fixed mortality terms (Bryant *et al.*, 1995). Thus, multispecies approaches or extended ecosystem models are indispensable to account for the full dynamics of predation impacts on zooplankton. A model that includes gelatinous carnivores in

addition to a single species (European anchovy) population model has been published by Oguz *et al.* (2008). The gelatinous carnivores were added to the model as a third functional zooplankton group that also preys upon early life stages of anchovy. The model has been successfully applied to the Black Sea ecosystem to study the interactions between anchovy and gelatinous zooplankton populations.

Multiple species HTL models

The IBM OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation) simulates individual fish interacting via an opportunistic predation process (Shin and Cury, 2001, 2004). This multispecies model enables the simulation of fish communities and has been dynamically coupled to a NPZD model by Travers *et al.* (2009). Predation mortality on plankton groups is then explicitly derived from the amount of plankton biomass effectively eaten by fish with respect to the available plankton biomass. The relatively small time-step of OSMOSE (15 d in the southern Benguela application) allows seasonal changes in the plankton community to be resolved, better representing the spatial-temporal dynamics of prey for the fish compartment. Indeed, a seasonal plankton peak induces seasonal variability in small pelagic fish, following Lotka–Volterra predator–prey dynamics. Furthermore, OSMOSE simulated the whole life cycle of fish, from eggs and larvae up to juveniles and adults. As predation is opportunistic and size based in the model, the predation intensity on plankton groups (defined by size ranges) varies according to fish ontology and growth. Travers and Shin (2010) could show that this fish-induced mortality rate on plankton was lower in locations of high plankton biomass (no food limitation for fish) and varies temporally following the time-lag existing between plankton production peak and the latter peak of small pelagic fish biomass.

Another example where a multispecies IBM (*C. finmarchicus*, and three planktivorous fish species) is coupled online to a LTL biogeochemical model is norwecom.e2e applied to the Norwegian Sea (Huse, 2005; Hjøllø *et al.*, 2012; Utne and Huse, 2012). In contrast to the OSMOSE example, zooplankton is not part of the biochemical model but has been explicitly parameterized as an IBM for *C. finmarchicus*. The fish model accounts for the most important planktivorous fish species in the system and allows resolving spatial and temporal dynamics of predation mortality from this predator group, whereas predation by invertebrates has been included basically as a function of light availability (day/night, depth). Zooplankton other than *C. finmarchicus* was included in the model assuming a constant background concentration.

Coupled LTL-multispecies models form a great tool to address the closure problem in LTL models and include spatially explicit predator–prey dynamics into simulated zooplankton estimates. But, the application of these types of models is challenging in several ways. The major constraint is the large number of parameters required to consider all biologically relevant processes in the model. This includes the physiological parameters concerning feeding, growth, assimilation, and reproduction (for a full life cycle model) as well as knowledge of species interactions and general migration strategies. Thus, the list of parameters can be quite long when the model attempts to simulate systems with a large number of species, which introduces more uncertainty in model estimates. Additionally, solving the model is associated with relatively high computational costs, which limits the model’s temporal and spatial resolution.

Fish functional groups

Another possibility to link HTL compartments to LTL models is to extend the LTL model by respective functional groups as proposed in Fennel (2008, 2009). In this approach, each targeted fish species is parameterized within the Eulerian framework and can hence easily be linked up to a LTL NPZ model. Fennel (2008, 2009) developed a model for the Baltic Sea where only three fish species (sprat, herring, and cod) represent 80% of the fish biomass. Variables relevant for fish need to resolve both biomass and abundance for several stages for each species, which potentially multiplies the number of state variables and the number of required parameters in the model. The predator–prey interaction between fish and their zooplankton prey were parameterized using an Ivlev functional response and additionally made temperature-dependent. Although the model is not yet set up in a spatial-temporal context, it has been used to simulate a 40-year hindcast period (1963–2003) and was shown to reproduce the main features of stock size and the magnitude of changes (Fennel, 2010). One major constraint of the aforementioned model is the explicit differentiation of the fish module into single species, which makes the correct parameterisation especially difficult in ecosystems with high (and changing) species diversity. This could, for example, be addressed by combining fish species into functional groups. In general, the approach is limited by the same constraints as the LTL-multispecies IBM approach. In both cases, the major zooplanktivorous species are simulated providing spatially explicit prey fields for zooplanktivores. However, in both cases, the closure term problem is shifted to the next, higher trophic level.

E2E modelling approaches

Along the same lines than previous modelling approaches (LTL–HTL coupling and extending model with fish functional groups), some homogeneous models aim to cover the full foodweb using similar representation for all organisms. EwE (Christensen and Walters, 2004) is one of the most widely applied E2E approaches to model marine foodwebs worldwide (Christensen et al., 2009; Fulton, 2010). The core of EwE is a mass-balance model Ecopath that provides a snapshot of functional group biomasses, foodweb structure, and flows of energy (Polovina, 1984; Christensen and Pauly, 1992). The time-dynamic model Ecosim uses Ecopath parameters as initial conditions and is suited for studying the direct and indirect (via trophic interactions) ecosystem effects of fishing and other environmental drivers. In Ecosim, the functional responses in feeding stem from the foraging arena theory (Walters, 1997; Plaganyi and Butterworth, 2004) and the trophic predator–prey relationships are either bottom-up, mixed, or top-down controlled depending on the prey vulnerability to predation. The user can define the level of detail in the description for each functional group. In existing model applications, zooplankton has been described at species level (e.g. Tomczak et al., 2012), in different size classes (e.g. Harvey et al., 2003), in functionally defined groups (e.g. herbivorous and carnivorous zooplankton, Okey et al., 2004), or as a single functional group (Zhang and Chen, 2007). In practice, however, EwE models tend to be fish-centric, and the LTLs are often described with low detail. Some examples exist where an EwE model has been linked to a biogeochemical (Meier et al., 2012), NPZ, and/or individual based zooplankton model (e.g. Aydin et al., 2005). Yet, only few examples exist of true, two-way coupling between EwE and a biogeochemical or NPZ model (Kearney et al., 2012). Without such coupling, the

top-down effects on zooplankton, where relevant, may be underestimated, as the HTL effects on phytoplankton production are only partially accounted for.

Another approach has been given by Fulton et al. (2003) where species are combined into functional groups. The model has been solved on a coarser spatial grid and with simpler hydrodynamics than traditional NPZ models, but it is flexible and faster to run, which makes it ideal for management purposes. The Atlantis model is a more complex biogeochemical-based E2E model and includes all trophic levels from phytoplankton to fish, benthos, mammals, and birds, as well as the human society (Fulton et al., 2003; Fulton, 2010). In the original formulation of the model, meso-zooplankton functional groups were divided into omnivorous and carnivorous. Since HTL predation by fish is explicitly represented in the model, predation mortality and mortality from other sources [referred to as “closure term” in Fulton et al. (2003); e.g. linear “basal” mortality, mortality by predator groups not represented in the model, oxygen-dependent mortality] are formulated separately (Fulton et al., 2003). For all functional groups, consumption in the standard set-up are parameterized with a Holling type II functional response (Holling, 1959), whereas the “closure term” is a combined linear and quadratic term. Fulton et al. (2003) demonstrated that the model is highly sensitive to changes in either of the mortality terms with stronger response to changes in the consumption formulation. But, since the model concept includes a large number of interacting functional groups, those sensitivity experiments prohibited identifying the actual implications for zooplankton only. Nonetheless, the study highlights the importance of the mortality terms for the solution of marine ecosystem models.

As mentioned above, E2E models tend to emphasize upper trophic levels rather than LTL production and zooplankton. They are usually more coarsely resolved giving a general overview on regional ecosystem dynamics rather than focusing on small-scale spatial-temporal variability in, for example, zooplankton mortality. Generally, the coupled E2E models indicate that the mass fluxes from zooplankton up to fish were significantly smaller than those within the NPZD model, but on longer time-scales, the feedback from fish predation may change foodweb dynamics of LTLs (Fulton et al., 2003; Megrey et al., 2007; Fennel, 2009; Travers et al., 2009).

One major challenge related to the coupling between lower and higher trophic level models is to determine the actual amount of zooplankton that is available as prey for the fish/HTL compartment, since LTL zooplankton biomass includes often a general, unspecific predation loss that needs to be corrected for. This demands that the models are coupled online to avoid inconsistencies due to the violation of required mass conservation. Furthermore, specific care needs to be taken when the trophic levels are solved with different time-steps.

Parameterization of “other” mortality terms

Depending on the complexity of the model system, various degrees of intra- and interspecific competition and intraguild predation are included. In lower trophic models with a limited number of zooplankton groups, intraguild predation can be described by assuming that a fixed fraction (Z_{frac}) of the biomass is subjected to intra-guild predation and that the rest ($1 - Z_{\text{frac}}$) is subject to predation by higher trophic levels (beyond zooplankton; Mitra, 2009). This approach appears to yield more realistic foodweb dynamics (Mitra, 2009), but does not take into account that Z_{frac} may vary seasonally and spatially. Foodweb models encompassing more zooplankton

groups are better in describing the intraguild predation and the response to external forcing at all trophic levels and hence marine ecosystem variability. However, the increase in model complexity may lead to larger demand on computational resources and, besides not having sufficient biological knowledge, there may also be difficulties related to defining useful starting fields for ocean state and all trophic levels as well as having appropriate field observations for verification and validating model results.

Discussion and conclusion

The published literature on the trophodynamic processes affecting the zooplankton community within six different ecosystems located around the Atlantic Ocean was reviewed. Emphasis was placed on documenting the importance of predation mortality experienced by zooplankton and to which degree the strength of this trophodynamic coupling changes temporally, spatially, or due to differences in physical or biological attributes of the ecosystem. Although the compilation was purely descriptive and the number of ecosystems included in the review was limited, comparison among the different ecosystems allowed us to identify commonalities and differences, and hypothesize systematic relationships between physical, geographical, or biological states of the system and its vulnerability to basic changes in trophic structure.

Trophic control in regional Atlantic ecosystems: general pattern

For two of the six ecosystems, North Sea and Bay of Biscay, there was little evidence that predators exerted top-down control on zooplankton. Both ecosystems exhibit high species diversity, moderate (temperate) temperatures, and a strong exchange to the open ocean. In contrast, the Baltic Sea and Norwegian Sea can be identified as “extreme” ecosystems with a relatively small number of zooplankton species and those species are exposed to rather extreme environmental conditions such as cold temperatures, potential ice cover, and, for the Baltic Sea, low salinities. In these ecosystems, potential top-down control situations for zooplankton were reported. The two remaining ecosystems, GB and the southern Benguela upwelling system, are characterized neither by limited species diversity nor by extreme environmental conditions. Nonetheless, top-down as well as bottom-up processes are equally important for shaping the population dynamics and size structure of the zooplankton community. Thus, we hypothesize that, at least for the ecosystems of the NEA, low species diversity and/or extreme environmental conditions increase the potential impacts of top-down control on zooplankton. This agrees with the hypotheses suggested by Frank *et al.* (2007) who, although mainly considering relationships between piscivorous fish and their prey, found correlations between the trophic status of an ecosystem and species diversity and temperature, with colder temperatures and lower species diversity leading to a higher probability of top-down regulation.

Importance of top-down control with respect to temporal and spatial scales

In none of the ecosystems zooplankton exhibited prolonged phases with dominant top-down control but in four ecosystems top-down processes were reported to play an important role in zooplankton dynamics. Generally, long-term changes in the zooplankton community, either in biomass or in size structure, were found in all six ecosystems. When comparing the different ecosystems, it was particularly notable that changes in the community size structure towards smaller species had occurred in at least three (North Sea,

GB/GoM, Benguela) of the six systems at about the same period (late 1980's) and, at the same time, a shift in the species dominance of the Baltic Sea zooplankton was observed. Nonetheless, no obvious commonalities in the underlying processes could be identified and relevant processes described in the literature range from abiotic controls to top-down processes. For the bottom-up structured ecosystems such as the North Sea, changes in mainly abiotic factors such as temperature and water circulation patterns were correlated with changes in the size composition. Fromentin and Planque (1996) already described the negative correlation between the North Atlantic Oscillation (NAO) and the predominance of the larger *C. finmarchicus* over the smaller *C. helgolandicus* in the eastern North Atlantic. The underlying processes are not yet quite clear, but possible candidates are “advection, modification of biotic interaction, impact on bottom-up control, delay of the spring bloom, and the effect of turbulence” (Beaugrand and Ibañez, 2000). In contrast, in the systems where zooplankton experience top-down control by predators (Baltic Sea, GB, Benguela), changes in the planktivorous fish community are a dominant force shaping the characteristics of the zooplankton community. Mechanisms underlying this relationship have already been described by Brooks and Dodson (1965) who formulated the “size-efficiency hypotheses” that links predation intensity to the zooplankton size structure assuming a size-dependent predation favouring larger over smaller zooplankton. The hypothesis has been further discussed by, for example, Hall *et al.* (1976). Another example on how bottom-up and top-down processes interact to structure the zooplankton size spectrum was given by Suthers *et al.* (2006) comparing impacts of nutrient intrusions (bottom-up) with that of size selective predation (top-down).

Despite the general trophodynamic pattern, predator–prey interactions cannot be considered homogeneous in space and time when looking at much smaller spatial and shorter time-scales. Even in mainly bottom-up controlled ecosystems, the zooplankton community within distinct spatial structures like fronts, river plumes, or retention areas can be potentially more strongly impacted by predation than the ecosystem in general. Furthermore, the seasonal dynamics of the ecosystem productivity can also change the trophic control on the zooplankton community as has been reported for Bay of Biscay, Baltic Sea, and the North Sea, where particularly in autumn the predation impacts potentially dominates over zooplankton production. More generally, our review indicates that, if the model at hand is supposed to capture the interactions between bottom-up and top-down effects, the spatial and temporal model resolution must be sufficiently high, as top-down effects may occur quite local and during short periods. Modelling studies and ecosystem analysis are in a different state of advancement between the six ecosystems, which potentially introduce a bias in the comparison of their functioning. Top-down effects, often being transitory, are in general more difficult to detect by observations. Thus, the oceanographic research community should increase efforts towards gathering larger datasets of longer time-series, as well as focus research efforts on more detailed analysis of mesoscale processes.

Requirements of models

As for many modelling challenges, the requirements for the parameterization of zooplankton predation mortality depend largely on the scientific question being addressed. deYoung *et al.* (2004) proposed a rhomboid approach for inter-trophic ecosystem models with highest resolution applied to the targeted trophic level (or

species) and decreasing resolution up and down the trophic chain with increasing distance to the key level. In contrast, [Mitra and Davis \(2010\)](#) already states that the zooplankton component “should not be simplified arbitrarily to higher and lower trophic levels”, but that model simplifications need to be “critically examined and quantified” with both theoretical studies and observations. Here, we propose some basic rules that can be followed when choosing a certain parameterization for a process or a specific trophic level. First, the process resolution must be chosen based on the most basic processes that need to be resolved to ensure a reasonable representation of all trophic level involved in addition to the hydrodynamic processes. Thus, the trophic control of an ecosystem can serve as an indication, on which processes and trophic levels are more relevant than others. Here, we can hypothesize that the processes controlling a trophic level need to be better resolved than those of lesser relevance for its dynamics. Which means for zooplankton predation mortality that the choice of the ideal parameterization would be different in the bottom-up controlled North Sea where the higher trophic levels play a lesser role on zooplankton dynamics, than, for example, in the “wasp-waist” controlled Benguela upwelling system where major top-down impacts can be expected and hence need to be resolved thoroughly. Second, the required resolution of a biological process depends also on the temporal and spatial resolution of the model. Third, the specific scientific purpose can give specifications on what process resolution is needed. For example, if one is interested in top-down effects on zooplankton one might not only need a reasonable resolution of the predator compartment but also of the zooplankton size classes, since zooplanktivorous predators show clear preferences to certain prey size ranges or prey quality ([Daan et al., 1990](#); [Munk and Nielsen, 1994](#); [Beaugrand et al., 2003](#); [Daewel et al., 2008b](#)). Taking this into account, we can discuss the probable resolution for the zooplankton predation term in relation to the trophic state of the system.

In general, it appears necessary, even in bottom-up controlled systems but especially in potentially top-down controlled systems, to find a dynamical representation for zooplankton closure, like, for example, in [Utne et al. \(2012a\)](#), their Figure 9) who simulated predation mortality of zooplankton along the Norwegian coast using an online coupled multispecies fish IBM. Another example was published by [Travers and Shin \(2010\)](#), who aimed at quantifying the feedback of fish predation on zooplankton in the Benguela. By coupling a biogeochemical model representing two groups of zooplankton (N2P2Z2D2 model by [Koné et al., 2005](#)) and the multispecies HTL model OSMOSE ([Travers et al., 2006](#)), the high spatial-temporal variability of fish-induced mortality on copepods was demonstrated. Applying the modelled variable predation mortality on the zooplankton model has two major consequences on its dynamics ([Travers et al., 2009](#)). First, although average zooplankton biomass is not highly impacted by the predation, the amplitude of the seasonal cycle is generally reduced, illustrating the theory that the abundance of predators dampens the variability of their prey ([Sala, 2006](#)). Second, the seasonal dynamics of the LTL ecosystem is affected by the variable fish-induced mortality, with prolonged copepod persistence in the system and a phenological shift of flagellates to an earlier bloom maximum. Finally, [Travers et al. \(2009\)](#) showed that the consideration of spatio-temporal variability of the mortality term on zooplankton has important and unpredictable effects on its dynamics. This study emphasizes the necessity of dynamic predation terms, but there are major constraints to the available approaches that limit their applicability. As already

stated earlier, those models need a complex set of information to be parameterised and, due to their complexity, they are computationally expensive. Although it is tempting to include a complex mechanistic model to account for predation losses, it is important to appraise whether the additional parameter uncertainties and the high computational costs are necessary in the targeted ecosystem and for the scientific question.

When particularly interested in zooplankton dynamics, the tool representing the HTL compartment does not necessarily need to resolve all individual species in the system but needs to be consistent with the zooplankton in terms of mass and energy conservation emphasizing the need to couple the trophic levels online to each other. Thus, it could likewise be derived from a size-structured approach ([Maury et al., 2007](#)) or includes predators assembled into functional groups (like, for example, in Atlantis [Fulton et al., 2004](#)). From the available literature, it becomes clear that there is no generic approach available that can solve the closure problem for zooplankton in ecosystem models or provide consistent links between zooplankton and HTL models. But, it underpins the necessity to consider several aspects (i.e. trophic control, spatial and temporal resolution, research focus) for model development. In highly vulnerable (to top-down impacts) ecosystems like the Norwegian Sea or the Baltic Sea, a dynamic coupling between predator and prey and a relatively high resolved predator compartment is highly recommended. In return, these systems are characterized by lower species diversity and in the two selected cases only few key players in the system, which makes it easier to parameterise the models. In contrast, in more stable ecosystems that are largely bottom-up structured (specifically in the North Sea and Bay of Biscay), more simplified solutions are applicable on coarser space and time-scales. Nonetheless, if the spatial resolution of the model is in the range of mesoscale processes like eddies or fronts and/or the temporal resolution capable for considering seasonal dynamics, the dynamical representation of predation on zooplankton needs to be considered. In systems with a large number of species, more general approaches for the HTL compartment (e.g. functional groups, size-structured) are likely more robust and easier to parameterize than multispecies models.

Additionally, the identification of top-down control on zooplankton in regional ecosystems is really difficult from the data available and only few methods focused explicitly on this topic (e.g. [Munk and Nielsen, 1994](#)). In other areas, additional model experiments helped to explain observed changes in zooplankton ([Ji et al., 2012a](#)). Here, we would like to emphasize the need of data acquisition at right scales to identify the predation impacts on zooplankton and to develop consistent process oriented modelling approaches required to close the link between zooplankton and HTL models.

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