Parameterizing and operationalizing zooplankton population dynamic and trophic interaction models

Introduction

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This themed set (TS) of articles was motivated by the need for modellers and biologists–ecologists to work more closely together to produce more realistic simulation models of zooplankton population dynamics and trophic interactions. The TS was intended to cover a broad range of subjects and potential approaches, including identifying crucial gaps in our knowledge and parameterization of biological/physiological processes, experimental/fieldwork aimed at quantifying the response of key physiological and behavioural processes to variations in the environment, identifying novel modelling approaches that would enable the development of simulation models that would minimize the need for species-specific (and stage-specific) model parameterization, etc. Five articles were accepted for inclusion in the TS. They cover the majority of these themes. TSs are intended to be instrumental in focusing attention, triggering opinions, and stimulating ideas, discussion and activity in specific research fields. We hope that this TS has achieved that.

Keywords: ecosystem models, habitat modelling, predator–prey interaction models, simulation modelling, zooplankton population dynamics, zooplankton biodiversity.

This themed set (TS) of articles was motivated by the need for modellers and biologists–ecologists to work more closely together to produce more realistic simulation models of zooplankton population dynamics and trophic interactions. The TS was intended to cover a broad range of subjects and potential approaches. Among the topics that we considered should be addressed were

(i) identify crucial gaps in our knowledge and parameterization of biological/physiological processes at the individual or population levels to optimize coupled biophysical models;
(ii) describe experimental/fieldwork aimed at quantifying the response of key physiological and behavioural processes to variations in the environment, a problem that depends on the temporal/spatial scale of model application (i.e. the finer the scale is, the greater the limitation);
(iii) identify novel modelling approaches that would enable the development of simulation models that would minimize the need for species-specific (and stage-specific) model parameterization and that would support the development of community-level models;
(iv) develop new approaches aimed at increasing our capacity to model zooplankton habitat to forecast potential changes in zooplankton spatial distribution in response to future climate change.

Five articles were accepted for inclusion in the TS. In addition, one of the articles (Record et al., 2014a) provoked a COMMENT (Cropp and Norbury, 2014) to which Record et al. REPLY (Record et al., 2014b)—both of these are included in the TS. As a whole, these contributions cover the majority of the themes in which we were interested.

Daewel et al. (2014) assessed to what level zooplankton dynamics in different marine ecosystems of the Atlantic Ocean are driven by predation mortality and how the latter is considered in existing modelling approaches. They conclude that predation mortality
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generally plays an important role in controlling zooplankton population dynamics, but its impact varied among the six ecosystems examined. The authors describe several methods of parameterizing zooplankton mortality in models, ranging from fixed mortality rates to complex coupled multispecies models. They conclude that modelling constraints must be balanced with the ecosystem-specific demand for a consistent and spatio-temporally dynamic implementation of predation mortality in any model’s zooplankton compartment.

A pair of companion articles demonstrates the need to better describe species-specific patterns of zooplankton diel vertical migration in response to variations in environmental conditions and the impact that these patterns have in three-dimensional transport models. Plourde et al. (2014) describe the species-specific response of daytime weighted mean depth (WMD) of two species of krill, Thysanoessa raschii and Meganyctiphanes norvegica, to variations in surface salinity and concomitant light attenuation. The WMD of T. raschii and M. norvegica were significantly and positively related to surface salinity (light), with M. norvegica observed deeper and in warmer water than T. raschii. Using these results as mechanistic functions regulating krill vertical position, Maps et al. (2014) used a three-dimensional coupled regional circulation model to quantify the differences in upstream advection resulting from the interaction between the circulation and the specific DVM of T. raschii and M. norvegica. They identified spatio-temporal patterns in krill upstream transport that differed in relation to the DVM behaviour exhibited by the different species of krill. These two articles illustrate the need to accurately parameterize first-order physiological/behavioural processes, such as DVM, to optimize modelling of species-specific transport and responses to environmental forcing.

Record et al. (2014a) present a novel approach to incorporate coexistence/biodiversity of zooplankton into ecosystem models. They suggest approaching the problem from the perspective of community-level patterns. The model allows for diverse assemblages of phytoplankton or zooplankton groups to persist and produces accurate community-level patterns. The approach is simple, adding only one additional parameter to existing models, and allows scientists to test the effects of trait distributions and environmental variables on diversity. The Record et al. (2014a) article prompted a COMMENT by Cropp and Norbury (2014). They discuss specific aspects of the mathematical mechanisms for coexistence proposed by Record et al. (2014a) and argue for the use of non-linear mortality terms to produce coexistence. Record et al. (2014b) respond, promoting a community-level approach to the problem that they say can offer valuable simplifications and insights.

Chust et al. (2014) present a new approach to verify the poleward shift of Calanus species and to assess how much of this shift was triggered by ocean warming. To achieve this objective, they compared the observed species-specific population gravity centre with that estimated from a series of generalized additive models using: (i) only climate factors to simulate species-habitat suitability, (ii) only temporal and spatial terms to reconstruct the population distribution, and (iii) both factors combined. They found that only C. finmarchicus consistently shifted poleward in response to sea warming, but at a lower rate than previously estimated in other work. The authors found that C. helgolandicus was expanding in all directions, although its distribution limit in the North Sea has shifted further north. This approach, supported by high model accuracy, demonstrated its usefulness in detecting species latitudinal shifts, and identifying its causes.

TSs are intended to be instrumental in focusing attention, triggering opinions and stimulating ideas, discussion and activity in specific research fields. We hope that this TS has achieved that.

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References


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Food for Thought

The paradox of the “paradox of the plankton”

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One of the central orienting questions in biodiversity theory and ecology is the “paradox of the plankton”, which asks how it is possible for many species to coexist on limited resources given the tendency for competition to exclude species. Over the past five decades, ecologists have offered dozens of solutions to the paradox, invoking game theory, chaos, stochastics, and many other concepts. Despite the plentitude of solutions to the paradox, ecologists continue to offer up novel solutions. Ocean modellers are now faced with the opposite paradox: given the overabundance and the diversity of solutions to the paradox, what is the appropriate way to build coexistence into ecosystem models? Ocean ecosystem models have a very standardized form—nutrient–phytoplankton–zooplankton (NPZ)-type systems of differential equations—where competitive exclusion is a common model behaviour. We suggest approaching the problem from the perspective of community-level patterns. We offer a prototype for building coexistence into NPZ models. The model allows for diverse assemblages of phytoplankton or zooplankton groups to persist and produces accurate community-level patterns. The approach is simple, adding only one additional parameter, and allows us to test the effects of trait distributions and environmental variables on diversity.

Keywords: biodiversity, ecosystem modelling, NPZ, paradox of the plankton, plankton.

Introduction

The standard ocean ecosystem model has changed very little since its design over 60 years ago. At the core is the nutrient–phytoplankton–zooplankton (NPZ) model, which describes the dynamics of those three state variables, as concentrations, using a system of three differential equations (Riley et al., 1949). Oceanographers have augmented this model with ~1–10 additional state variables, describing other important quantities, such as the detritus concentration, or the concentrations of multiple functional groups (Chai et al., 2002), and these augmented models, coupled with fluid dynamics models, form the basis for global and regional ocean ecosystem studies.

The simplicity and the generality of NPZ models make them a useful tool for global and basin-scale modelling studies. However, many important ecosystem shifts are not represented in this modelling approach. For example, the introduction of a single species (e.g. Mnemiopsis leidyi, Kideys, 2002) can restructure planktonic and fish communities. Even shifts in the relative proportions among native species within a trophic group can restructure higher and lower trophic levels (Pershing et al., 2005). Similarly, diversification within models can add fundamentally new behaviours (Gentleman et al., 2003). To account for these processes, we must incorporate some aspect of biodiversity into our models.

There are sophisticated models for incorporating biodiversity into terrestrial systems (cf. Hubbell, 2001), and many ecologists have assumed that terrestrial biodiversity principles will apply directly to oceanic systems (Hooper et al., 2005). In general, these models are designed for sessile systems and do not mesh easily with fluid systems or the NPZ framework. Furthermore, there is evidence that biodiversity operates in fundamentally different ways in pelagic ecosystems when compared with terrestrial and benthic...
One of the roadblocks to extending NPZ models to better represent properties like biodiversity is the well-studied "Paradox of the Plankton" (Hutchinson, 1961, hereafter "the Paradox"). The Paradox is one of the central orienting concepts in ecology. It is the conflict between the classical theory, which predicts competitive exclusion (Volterra, 1928; Lotka, 1932), and the observation of nature, which supports the coexistence of a diversity of competitors.

In other words, classical theory predicts that $n$ resources can support at most $n$ species, with all additional species vanishing due to outcompitition; yet in planktonic systems, a smaller number of resources can support many species. NPZ models have their roots in Lotka–Volterra functional forms, so that competitive exclusion is still the primary behaviour in ocean foodweb models, particularly when each trophic level has multiple compartments (Cropp and Norbury, 2012). To represent community properties in these models, there must be some mechanism for coexistence.

In the five decades since Hutchinson posed the Paradox, ecologists have offered myriad plausible solutions to the Paradox. Early solutions included alternate functional forms (Lotka, 1932) and fluctuations in environmental conditions (Hutchinson, 1961). The list has grown, and there are a number of extensive reviews of solutions to the paradox. Wilson (2011) reviewed a series of reviews which categorized roughly 50 separate mechanisms for coexistence, and there are still more one could add to this list (e.g. Pachepsky et al., 2001). The abundance of viable solutions to the Paradox poses a pragmatic problem to ocean modellers. Incorporating these many mechanisms for coexistence would require extensive parameterization, vastly increased uncertainty, and a much improved understanding of interactions among countless combinations of species. However, incorporating just one or two mechanisms would bias the model towards these mechanisms, and there is currently little evidence that a single mechanism allows for coexistence across global, multitrophic ocean ecosystems and across a range of spatial and temporal scales. Thus, models are left with a dilemma: given the overabundance of solutions, what is the appropriate way to build coexistence into NPZ-type models? We view this dilemma as "the paradox of the 'paradox of the plankton'" (hereafter "Paradox II").

Coexistence likely arises via a combination of multiple mechanisms, which vary spatially, temporally, and by trophic group. We require an alternative to representing and parameterizing every mechanism. One approach is to formulate a term that captures the aggregate behaviour of many mechanisms. By analogy, consider common representations of mortality within a single-species model. There are multiple sources of mortality for this species (e.g. predation, starvation, injury, viruses), and few models represent these many processes explicitly. Rather, one or two simple mortality terms aggregate these many processes. Similarly, a single population growth term aggregates processes including mobility, perception, ingestion, assimilation, metabolism, and others. We propose using an analogous approach to build coexistence into NPZ models. This approach would entail adapting the current NPZ models to allow for coexistence in a general way. We suggest two criteria: (i) the functional form should be simple, with few parameters and (ii) the model should reproduce observed patterns at the community level. In other words, it is standard in most models to validate against the abundance of individual species. Here, we place greater emphasis on validating against the properties of the community, such as dominance–diversity patterns. We present a prototype for this approach. We introduce a functional form that meets these criteria and discuss how this type of function can mesh with other ecological approaches, such as trait-structured modelling.

**Prototype model**

We demonstrate our approach by focusing on the mortality term in the $Z$ equation. This allows us to demonstrate a prototype in the simplest mathematical context. The approach we use applies equally well to the phytoplankton equation or to grazing, and more generally to consumer–resource equations. We begin with the standard NPZ model,

\[
\frac{dN}{dt} = -f \left( I^g(N)P + (1 - \gamma h(P)Z + i(P)P + j(Z)Z \right)
\]

\[
\frac{d\rho}{dt} = f \left( I^g(N)P - h(P)Z - i(P)P \right)
\]

\[
\frac{dZ}{dt} = \gamma h(P)Z - j(Z)Z
\]

where $f$, $g$, $h$, $i$, and $j$ are the functional responses, $I$ the irradiance, and $N$, $P$, and $Z$, respectively, the nutrient, phytoplankton, and zooplankton concentrations (Franks, 2002). To isolate the zooplankton equation, we assume that food is saturated, and we simplify the population growth term to a constant, $\gamma$. This gives us a generic consumer–resource equation. We can extend this equation to include biodiversity properties by allowing for many $Z_i$ classes (cf. Armstrong, 1994),

\[
\frac{dZ_i}{dt} = \gamma_i Z_i - j(\bar{Z} \cdot Z_i)
\]

where $\bar{Z} = [Z_1, Z_2, \ldots, Z_n]$, and $n$ is chosen based on either the richness of the community in question or computational considerations. The density-dependent mortality ($j$) could depend on either the entire population of zooplankton or the population of just the $i$th class. Realistically, mortality depends on a combination of the two, as some sources of mortality apply only to a single species, whereas others apply to many species in a community (e.g. a generalist predator or competition for a common resource).

For a single $Z_i$ class, a typical mortality term is the quadratic, $j(Z)Z = \mu Z^2$. In the biodiversity model, this would give

\[
\frac{dZ_i}{dt} = \gamma_i Z_i - \mu Z_i^2
\]

which is equivalent to a logistic model for each taxon, with no interaction between taxa, and a carrying capacity of $\gamma_i/\mu_i$ (Figure 1a). This approach produces an independent food chain for each taxon without any interaction or interdependence between species—essentially a collection of single-species models. A simple modification to provide interaction is to allow the mortality to depend on the density of the whole population in a similar way. That is,

\[
\frac{dZ_i}{dt} = \gamma_i Z_i - \mu Z Z_i
\]

where $Z = \sum_i Z_i$. This option produces competitive exclusion,
however, where all $Z_i$ approach zero, except for one, which approaches a finite limit (Figure 1e). This is the multispecies extension of the two-species competitive exclusion phenomenon.

We interpret these two cases as limiting cases. We desire an intermediate case where competition has a structuring effect on the community, but does not exclude all but one species. Additionally, the model should be general enough that we do not have to parameterize every possible interaction. As a prototype, consider the functional form,

$$
\frac{dZ_i}{dt} = \gamma_i Z_i - \mu_i Z_i^{1-\phi} Z_i^{1+\phi}
$$

(7)

If $\phi = 0$, this reduces to Equation (6), and if $\phi = 1$, this reduces to Equation (5). Intermediate values, $0 < \phi < 1$, represent varying degrees of competition. The equilibrium solution for $\phi > 0$,

$$
Z_i^* = \left( \frac{\gamma_i}{\mu_i} \right)^{1/\phi} \left[ \sum \left( \frac{\gamma_i}{\mu_i} \right)^{1/\phi} \right]^{-1}
$$

(8)

shows that this formulation produces the two desired behaviours. First, communities of species persist indefinitely (Figure 1b–d). Second, the trajectory of each species depends on the trajectories of the others. We have added only one new parameter, $\phi$, which represents a community property: the degree to which competition structures the relative abundance of each taxon. Thus, we have met our first criterion, of a simple formulation, not biased towards any mechanism for coexistence.

At the community level, there are a number of ways to organize biodiversity data. We draw examples from the unified neutral theory of biodiversity (Hubbell, 2001)—a predominant biodiversity theory, which aims at explaining biodiversity patterns by assuming that stochastic processes determine the success of individuals within a species. The unified neutral theory has good predictive power in many sessile systems, but is also the subject of much controversy. Here, we use this theory mainly as a reference point to discuss the basic properties of community-level patterns and for comparison with our approach. We draw two main examples of community-level patterns from the unified neutral theory.

The first example is the rank-abundance curve. When species abundance is plotted against species rank in abundance, the curve generally has a characteristic "S-shape", with more diverse communities having a flatter S-shape than less diverse communities (Hubbell, 2001: cf. Figures 5.1, 5.2, and 5.5). The $\phi$ mortality term produces an identical pattern (with $\gamma_i$ and $\mu_i$ drawn randomly from normal distributions). The parameter $\phi$ then determines the steepness of the curve (Figure 2a)—i.e. filling a role analogous to the fundamental biodiversity number $\theta$ (Hubbell, 2001). The second example is the abundance–distribution curve, which is a histogram of species organized by abundance class (divided logarithmically). When community sampling is thorough, this curve typically has a left-skewed lognormal distribution—i.e. there are more rare species than a symmetrical lognormal distribution would predict (Hubbell, 2001, cf. Figure 5.4). The $\phi$ mortality term produces this pattern as well (Figure 2b). As with the unified neutral theory, the structure of the emergent community is not strongly dependent on $n$.

A third community-level pattern, which is often overlooked in the biodiversity literature for sessile systems but is crucial to modelling planktonic ecosystems, is the persistence of cyclical seasonal patterns of abundance. As a simple demonstration, we have added a food-dependence (Michaelis–Menten) and a temperature-dependence (Arrhenius) to Equation (7),

$$
\frac{dZ_i}{dt} = \gamma_i \frac{P}{P + K_i} e^{-E_i (kT)} Z_i - \mu_i Z_i^{1-\phi} Z_i^{1+\phi}
$$

(9)

where $k$ is Boltzmann’s constant, and half-saturation coefficients ($K_i$) and activation energies ($E_i$) are traits drawn randomly from normal distributions. The population trajectories approach a stable seasonal cycle of abundance, with different species peaking at different times of year, and multiple species coexisting (Figure 3).

**Discussion**

Ecologists approach model building from a variety of different levels of organization. The classical ecological theory begins at the species level, where the priority is to reproduce the patterns observed regarding species population trajectories. This is the approach underlying NPZ models. One might also begin at the community level, where one of the first-order goals is to reproduce patterns observed at the community level, such as rank-abundance curves, or the dominance of a certain trait. These two approaches are not mutually exclusive, and by incorporating the latter into model building efforts, we may be able to improve our predictions.
of ecosystem dynamics at the community level. This could add to our understanding of biodiversity in dynamic systems like the ocean and may inform system level objectives such as ecosystem-based management.

Within the ocean ecosystem modelling community, there has been a push to include better representations of biodiversity. Modellers have observed that diversification within a model can add important and fundamentally new behaviours to the model (Gentleman et al., 2003). Moving away from the NPZ-type systems of differential equations would require the major restructuring of ocean ecosystem models, and at present, there is no clear alternative. Thus, it would be useful, in light of Paradox II, to have a general functional mechanism for coexistence. A $\phi$-type mortality term, like the one we have proposed, illustrates one method for overcoming Paradox II. It provides for stable, coexisting population trajectories and realistic community-level patterns, without burdensome parameterizations, and without giving preference to one of the many known mechanisms of coexistence.

The $\phi$ model differs from neutral biodiversity models in that it allows for trait-based differences between species. Despite this basic difference, the $\phi$ mortality term produces very similar patterns to the unified neutral theory of biodiversity. This similarity is essentially due to the structure of the randomness (i.e. Gaussian) underlying the processes in both models. In the unified theory, dispersal follows a random walk. For the $\phi$ mortality term, coefficients ($\gamma$, $\mu$) were chosen from random Gaussian distributions. For NPZ models, the coefficients typically represent organismal traits. The population growth term, for example, might include a formulation with measurable traits, such as a half-saturation coefficient, a $Q_{10}$ value, or a metabolic activation energy. The community-level patterns that emerge from the $\phi$ model are thus a direct consequence of the distribution of these traits. It is reasonable to expect that some traits are not distributed normally across communities, and we would therefore expect different community-level patterns.

Ecologists have measured the distributions of such traits across species and communities (e.g. Record et al., 2012), and there is increasing recognition of the need to improve this type of knowledge for planktonic communities in the ocean (Barton et al., 2012).
This growing body of knowledge of planktonic trait distributions provides the potential to parameterize the traits in a $\phi$-type model. Values of $\phi$ can be similarly estimated empirically by fitting to rank–abundance curves (Figure 2a), if the distributions of traits are known. A $\phi$-type model thus potentially provides a tool to test the link between the distribution of traits and the structure and properties of the community. One could, for example, examine how a shift in the distribution of a temperature-dependent trait such as activation energy could restructure communities as the environment warms.

Trait-structured modelling approaches have recently produced promising results in global ocean planktonic ecosystem models. In an approach pioneered by Follows et al. (2007), the NPZ framework is extended to include multiple phytoplankton types, distinguished by randomly parameterized traits. Emergent communities are composed of those types that coexist in a given environment. In these models, coexistence among phytoplankton types is buffered by a reduction in fitness differences between types, referred to as an “equalizing” mechanism for coexistence (Chesson, 2000). Competitive exclusion is still an intrinsic model property, but the rate of exclusion is sufficiently slowed. The addition of a $\phi$-type term would provide a stabilizing effect to this type of trait-structured model, with the ability to dial up or down the degree to which competition structures the community.

We have demonstrated the $\phi$ mortality term on the zooplankton equation for clarity, and it produces similar results when applied to the phytoplankton equation. There are other terms that could fill a similar functional role in NPZ models. The $\phi$ mortality term is designed to be a simple prototype for this approach. It allows us to produce coexistence and realistic community-level biodiversity properties. It does not preclude the addition of more specific modes of coexistence if they are known to be dominant influences. As the field advances, and our understanding of coexistence mechanisms improves, we expect ecologists to develop improved formulations. Meanwhile, a $\phi$-type mortality term provides a solution to Paradox II, allowing us to incorporate biodiversity into NPZ models in a simple, realistic, and general way and providing a path to better understand how physical processes and trait distributions might influence community structure in the plankton.

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References


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Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach

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In the last decade, the analysis based on Continuous Plankton Recorder survey in the eastern North Atlantic Ocean detected one of the most striking examples of marine poleward migration related to sea warming. The main objective of this study is to verify the poleward shift of zooplankton species (*Calanus finmarchicus*, *C. glacialis*, *C. helgolandicus*, *C. hyperboreus*) for which distributional changes have been recorded in the North Atlantic Ocean and to assess how much of this shift was triggered by sea warming, using Generalized Additive Models. To this end, the population gravity centre of observed data was compared with that of a series of simulation experiments: (i) a model using only climate factors (i.e. niche-based model) to simulate species habitat suitability, (ii) a model using only temporal and spatial terms to reconstruct the population distribution, and (iii) a model using both factors combined, using a subset of observations as independent dataset for validation. Our findings show that only *C. finmarchicus* had a consistent poleward shift, triggered by sea warming, estimated in 8.1 km per decade in the North Atlantic (16.5 per decade for the northeast), which is substantially lower than previous works at the assemblage level and restricted to the Northeast Atlantic. On the contrary, *C. helgolandicus* is expanding in all directions, although its northern distribution limit in the North Sea has shifted northward. *Calanus glacialis* and *C. hyperboreus*, which have the geographic centres of populations mainly in the NW Atlantic, showed a slight southward shift, probably responding to cool water penetrating southward in the Labrador Current. Our approach, supported by high model accuracy, shows its power in detecting species latitudinal shifts and identifying its causes, since the trend of occurrence observed data is influenced by the sampling frequency, which has progressively concentrated to lower latitudes with time.

**Keywords:** *Calanus*, climate change, habitat model.

**Introduction**

Data from Continuous Plankton Recorder (CPR) survey in the Northeast Atlantic Ocean indicate that zooplankton exhibit distribution range shifts in response to global warming that are among the fastest and largest of any marine or terrestrial group (Beaugrand et al., 2002; Lindley and Daykin, 2005; reviewed by Richardson, 2008). Habitat models based on CPR data have also been developed to provide projections of future climate-driven shifts (Helaouet and Beaugrand, 2007, 2009; Beaugrand et al., 2008; Helaouet et al., 2011; Reygondeau and Beaugrand, 2011). Factors that control the spatial distribution of populations can be grouped into two main categories, external and internal (Planque et al., 2011). External controls, which are often referred to as environmental controls, are independent of population state, and they are the basis of the ecological niche theory (Hutchinson, 1957). Different statistical and mathematical techniques have been developed to model the spatial distribution of species, also termed species distribution models (Elith and Leathwick, 2009), climate envelope models (Pearson and Dawson, 2003), habitat distribution models (Guisan and Zimmermann, 2000), or habitat suitability models (Hirzel et al., 2002). A climate envelope model generally characterizes a set of suitable habitats for a species derived from their present geographic location. As, in general, habitat models are constructed from the associations between the extant geographic
position of a species’ occurrence and its climate, there is difficulty in testing these models under different climates (Lawing and Polly, 2011).

The second type of factors affecting the spatial distribution of populations is the internal control, which are directly linked to the population prospects (reproduction, mortality and migration rate, that for copepods is mainly based on advection). These include density-dependent processes, the effect of demographic structure, and biogeographical processes (Ohman and Hirche, 2001; Planque et al., 2011). These two factor types have traditionally differentiated both the conceptual view of species control (niche theory vs. population dynamics) and the modelling approaches (habitat models vs. individual-based models; Runge et al., 2005). When modelling the pelagic habitat of plankton, dispersal limitation is often neglected, although it can play an important role on community structure (Irigoien et al., 2011; Chust et al., 2013). Research efforts need to focus on integrating the two mechanisms in the modelling approach for zooplankton species, as attempted for fish and invertebrates (Cheung et al., 2009).

Time-series of spatially explicit biological data such as zooplankton occurrence are challenging to analyse because of non-uniform sampling across time and space. Very few predictive models have been validated using independent data (but see Lewis et al., 2006; Llope et al., 2012). Past works showed shift of populations (zooplankton assemblages) based on northward/southward limits of a restricted region (Northeast Atlantic) and did not encompass the overall distribution range of species (e.g. Beaugrand et al., 2002). Therefore, data reconstruction methods and models encompassing all North Atlantic and including both niche and population factors are needed to avoid bias in trend analysis and to explore possible causes of population shifts. The application of habitat models to case species also requires key steps to be accurately undertaken to avoid model overfitting (Burnham and Anderson, 2002), such as the selection of the explanatory variables and model validation. Model validation is one of the critical steps to extrapolate models to conditions outside of those used to generate the model, such as to other regions (Valle et al., 2011) and to future climate (Lawing and Polly, 2011).

Our objective is to develop models of habitat suitability (at species level) and data reconstruction for analysing past changes in zooplankton species (e.g. Calanus spp.) due to prominent climate drivers, particularly sea warming within the North Atlantic (Figure 1), using Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990). Zooplankton are good indicators of climate change for several reasons (Richardson, 2008): highly sensitive to temperature, most species are short-lived so there can be tight coupling of climate and population dynamics, copepods are usually not commercially exploited avoiding confusion with trends in exploitation, and the distribution of zooplankton can accurately reflect temperature and ocean currents because plankton are free floating. In this work, habitat suitability models were built for each one of the four copepod species (Calanus finmarchicus, C. glacialis, C. helgolandicus, and C. hyperboreus) within the temperate to Subarctic North Atlantic from 1959 to 2004. These species, especially C. finmarchicus, dominate zooplankton biomass in N. Atlantic; as one of the main grazers they transfer energy from phytoplankton to higher trophic levels such as commercially exploited fish (Planque and Batten, 2000; Richardson, 2008). The aim of this paper is to test whether population gravity centres of key taxa such as Calanus spp. shift poleward, and if so to explore whether this movement could be associated with sea warming. To this end, we compare time-series of observed data with a series of GAMs as numerical experiments: (i) a model using only temporal and spatial terms, as a data reconstruction method, to simulate population movement, (ii) a model using only climate factors (i.e. niche-based model) to simulate the habitat suitability, and (iii) a model using both climate and spatio-temporal factors combined. Subsequently, for all the models, the distribution of the species was predicted over the whole spatio-temporal domain. Thus, the rate of change of the geographic gravity centre of the modelled occurrence probability allowed us studying the shifts of the species population and habitat suitability along time.

Material and methods
Biological data and sampling frequency
Data on the abundance [mean density (ind. m$^{-2}$)] of four species (C. finmarchicus, C. glacialis, C. helgolandicus, C. hyperboreus), total diatoms and dinoflagellates, and the phytoplankton colour index (PCI) were obtained from the CPR database. The CPR survey is an upper layer plankton monitoring programme that has regularly collected samples, at monthly intervals, in the North Atlantic and adjacent seas since 1946 (Warner and Hays, 1994). Water enters the CPR through a small aperture at the front of the sampler and travels down a tunnel where it passes through a silk filtering mesh of 270 μm before exiting at the back of the CPR. The plankton filtered on the silk is fixed to a final concentration of 4% formalin into a tank within the CPR body. On return to the laboratory, the silk roll is unwound and cut into sections corresponding to 10 nautical miles (~3 m$^2$ of seawater filtered), the greenness of the silk is assessed and the plankton microscopically identified (Jonas et al., 2004). The CPR data used in the present study represent monthly data collected between 1959 and 2004 within 35 to 65°N and 75°W to 9°E. Data were gridded using the inverse-distance interpolation method (Isaaks and Srivastava, 1989), in which the interpolated values were the nodes of a 1° by 1° grid. Total diatoms and dinoflagellates represent an aggregation of data from 66 and 39 genera, respectively. Calanus glacialis and C. hyperboreus are Arctic species, whereas C. finmarchicus is a Subarctic species and C. helgolandicus dwells on temperate regions (Beaugrand et al., 2002). Calanus finmarchicus overlaps in size range with C. helgolandicus and C. glacialis which is the largest among them. The C. finmarchicus, C. helgolandicus, C. glacialis, and C. hyperboreus data here used are represented by the fifth copepodite and adult stages (i.e. CV-CV1). We use the PCI, which is a visual assessment of the greenness of the silk, as an indicator of the distribution of total phytoplankton biomass across the Atlantic basin (Batten et al., 2003; Richardson et al., 2006). This index covaries positively with both fluorimeter and satellite measures of chlorophyll (Batten et al., 2003; Raitos et al., 2005).

A non-uniform distribution of sampling in space and time might influence the subsequent analysis of the poleward shift of species population gravity centres. Therefore, sampling frequency have been analysed as a function of year, latitude, and longitude to test the uniformity of sampling effort over the period.

Environmental data and climate variability
Environmental data compiled had a spatial resolution of 1° longitude and 1° latitude and cover the entire domain defined. Sea surface temperature (SST), salinity, vertical velocity, and sea level anomaly were extracted from the reanalysis OS3 ECMWF (European Centre for Medium-Range Weather Forecasts) model and downloaded from CliSAP-Integrated Climate Data Center
Bathymetry was extracted from the ETOPO1 global model (NOAA). The time-series trends of SST were analysed over the period 1959–2004 to test whether isothermals increased at all latitudes. In addition, the overall mean SST was analysed over the period and map differences between cold and warm periods were calculated.

Habitat modelling and occurrence reconstruction

The approach consisted in modelling the species occurrence as a function of environmental factors (SST and salinity, vertical velocity), surrogates of environmental factors and population features (latitude and longitude, month), temporal trend (year), and potential food resources (PCI, total abundance of diatoms and of dinoflagellates), using GAMs (Hastie and Tibshirani, 1990). GAMs enable the fit of non-linear models for a wide family of statistical distributions. The presence/absence of each Calanus spp. was assumed to follow a binomial error distribution and the logit was considered as the link function. Overfitting was prevented by restricting the degrees of smoothness as explained below and by visualizing the response for each variable. The CPR dataset encompasses 178 910 samples across the spatial domain and irregularly distributed at year and monthly basis (see 2004 data as an example in Figure 1).

SST and salinity were used because of their recognized influence, either direct or indirect, on the spatial distribution of Calanus spp. (e.g. Helaouet and Beaugrand, 2007). Vertical velocity was used as a surrogate of upwellings. For environmental variables, the degree of smoothness of model terms was restricted from 3 to 5 to assume a unimodal niche model (sensu Hutchinson, 1957), but allowing asymmetry since interactions between species and extreme environmental stress may cause skewed responses (Oksanen and Minchin, 2002). In this sense, GAMs provide a more realistic solution than rectilinear climate envelope models or ellipsoidal climate envelope GLMs (Oksanen and Minchin, 2002). The CPR phytoplankton indices (i.e. PCI, diatoms, and dinoflagellates abundance) were tested individually as phytoplankton is a key food resource for Calanus spp. (Irigoien et al., 1998); however, because the data relative to these indices were not always available to cover the spatial and temporal domain as the other environmental variables, they were not used for spatial and temporal reconstruction of the habitat suitability model and they were not included in the overall model.

Month and geographic variables (i.e. latitude and longitude) are considered here as surrogates of population features or environmental factors not considered (Legendre, 1993). For instance, spatial terms might be proxies of overwintering areas, since close vicinity to an overwintering site has been suggested to be the main prerequisite for a region or water mass to hold a large population of C. finnarchicus (e.g. Head et al., 2000; Speirs et al., 2004; Torgersen and Huse, 2005). Spatial terms (i.e. latitude and longitude) were considered with interaction and using a bivariate smooth function. Month information was considered as a categorical variable; thus, a parametric coefficient was estimated for each month. To analyse the temporal trend, year was considered as explanatory variable and its GAM smoothness term was restricted to 5 degrees of freedom.

We built and compared three different models for each species. (i) A spatial and temporal model. A GAM using spatial (latitude, longitude) and temporal (month, year) terms only. This model is employed as data reconstruction method, thus, to identify trends on population over the analysed period. (ii) An SST model. A GAM based on only SST. As this model is driven by SST trend, it serves to identify species habitat suitability shifts. The comparison of the output of this model with the previous one permits to verify whether populations have shifted due to sea warming or if only their habitat suitability has shifted. (iii) A combined model. A GAM based on spatial, temporal, and environmental factors. As this model incorporates all factors, it has the potential to be the most accurate in predicting overall habitat suitability among the three model types, and it is used also to assess the relative contribution of spatio-temporal factors with respect to the environment.

Figure 1. The North Atlantic basin. The domain of the studied area is 35° to 65° N and 75° W to 15° E. Source of Bathymetry: ETOPO1, NOAA, Amante and Eakins (2009). Transparent dots are those sampled in the overall period (1959–2004). Red dots are those sampled in 2004.
Several steps had been undertaken: first, we have built a GAM for each variable independently. Second, we have selected the best model by removing variables that are not statistically significant or explaining the deviance of species occurrence by <1%. The explained deviance, $1 - \frac{\text{residual deviance}}{\text{null deviance}}$, is the equivalent to $R^2$ in least-squares models (Guisan and Zimmermann, 2000). Third, we have improved the model using an iterative procedure that is repeated five times. An iterative procedure that is repeated five times.

Model validation
We validated the models based on the cross-validation resampling procedure, which use independent datasets for model building and model validation (Burnham and Anderson, 2002). The comparison between the accuracy of the model (that using all observations to build the model) and that of cross-validated permits the detection of model overfitting, which highly reduce the use of such models for extrapolation. In particular, we used k-fold partitioning of a dataset (Hijmans et al., 2012), where each record in the dataset is randomly assigned to a group. In our case, group numbers are between 1 and k, with $k = 5$, hence, 80% of the CPR observations are used for model building, and the remaining 20% (i.e. independent) observations are used for model validation in an iterative procedure that is repeated five times.

The accuracy of the model and the five replicate model cross-validations have been evaluated using area under the receiver operating characteristic curve (AUC; Fielding and Bell, 1997; Raes and Steege, 2007) and accuracy indices derived from the confusion matrix (VanDerWal et al., 2012). To this end, first, the modelled probability of species presence was converted to either presence or absence using probability thresholds obtained using two criteria: sensitivity (true predicted presences) is equal to specificity (true predicted absences), and maximization of sensitivity plus specificity, following Jimenez-Valverde and Lobo (2007). Given the defined threshold value, a confusion matrix (also called an error matrix, Congalton, 1991), which represents a cross-tabulation of the modelled occurrence (presence/absence) against the observations data, was calculated. An overall accuracy measure was computed from the confusion matrix which is the proportion of the presence and absence records correctly identified. Both overall accuracy and AUC values range between 0.5 (random sorting) and 1 (perfect discrimination).

Time-series analysis of the geographic gravity centre
For all three model types, the probability of species occurrence was predicted over the whole spatial and temporal domain. Subsequently, we computed the geographic gravity centre of the predicted maps of probability of the presence of each species from January 1959 to December 2004. The gravity centre is defined as the mean geographic location of a population (Woillez et al., 2009). The changes in the gravity centre’s coordinates (longitude and latitude) were used to describe the changes in the geographic distribution of the habitat suitability in the Calanus spp. along time. As a way to test the sensitivity of this approach to detect geographic shifts triggered by environmental change, first, this statistic was calculated from the habitat suitability models for each time-step (i.e. a month) and subsequently represented along the seasonal cycle. Latitudinal trends estimated from these three models were compared with observed data (both abundance and presence/absence data) and sampling frequency.

RESULTS
Climate variability and change
The analysis of time-series over the period 1959–2004 indicated that SST at all latitudes analysed increased between 0.0240 and 0.0088°C year⁻¹ ($p < 0.0001$, $p = 0.018$, respectively). Specifically, the warming period started mainly at circa 1970 with a rate of increase of 0.028°C year⁻¹ ($p < 0.0001$) as showed by the mean SST (Figure 2a). The spatial difference of SST between cold (1969–1979) and warm (1998–2004) periods (Figure 2b) showed that warming in the NE Atlantic was more heterogeneous than in the NE Atlantic with three hotspots of warming and a region of slight cooling.

CPR data sampling frequency
Sampling frequency has a strong variability throughout years, with maximum effort in the 1960s and minimum in the 1980s (Figure 3a). The mean sampling frequency at the beginning of the period is more concentrated in higher latitudes and decreases 3° on average over the period, with moderate variability (Figure 3b). The mean sampling frequency is more concentrated in the eastern part of the North Atlantic during 1959–1961 and during 1987–1989 and in the western part in the remaining period (Figure 3b). There is a non-linear trend in the sampling frequency for the geographic longitude along the period.

Habitat models
First, each term (environmental, spatial, or temporal) was separately tested for each species using the GAM (Table 1). This indicates that the PCI and the total abundance of diatoms and dinoflagellates

![Figure 2.](image-url)
accounted for a limited deviance of species occurrence. Subsequently, the three model types were fitted to each species according to the methodology described and the explained deviance compared. In all *Calanus* spp., spatial and temporal models accounted for 33–45% of species occurrence, whereas environmental variables accounted for 17–31% (Supplementary SI1). Specifically, the SST model explained between 26 and 10% of the variation according to species. Environmental factors contributed very little to the combined

Figure 3. Sampling frequency as a function of year (a), as a function of year and latitude (b), and as a function of year and longitude (c). In (b) and (c), the size of the circle is proportional to the sampling frequency, the black line indicates the mean value at the corresponding year, and the dotted line indicates the linear temporal trend.
model (adding 0.9–2.2% to the explained variance), indicating that high covariation exists between both variables and types and that spatial and temporal terms are key to reconstruct habitat suitability over the period. For the combined model, the estimated degrees of freedom, p-value for each selected variable, and the accuracy measures of cross-validation are indicated in Table 2. According to the AUC and overall accuracy, models for C. finmarchicus, C. glacialis, and C. helgolandicus have good agreement between occurrence predictions and observations (AUC: 0.77–0.88 and overall accuracy: 78–79%), whereas that for C. hyperboreus was slightly less accurate (AUC: 0.72, overall accuracy: 72%). The high accuracy values for cross-validated models, also compared with that of model using all observations (80–90%), indicate that models do not present overfitting. As an example, Figure 4 shows the GAM response curves of the combined model for C. helgolandicus occurrence probability, whereas Figure 5 shows the SST model compared with the spatial and temporal model for the same species in June, averaged by periods. In particular from the SST model, it appears that the habitat suitability of C. helgolandicus at the southern limit nearby the Bay of Biscay shifted poleward from the 1970s to the 2000s, whereas the spatial and temporal model indicates a general expansion of the population in all directions, southward, northward, and offshore.

**Seasonal analysis**

To assess if the gravity centre index used is a good descriptor of the shift, first, the indices were applied to the Calanus spp. populations from the habitat suitability models (combined model) for each time-step (i.e. a month) then represented along the seasonal cycle (Figure 6). Population gravity centre shifts poleward from April to August (average for the overall 1959–2004 period) and southward from September to February. This pattern is consistent in all four species, with low differences in the magnitude of this shift (i.e. from 2° of latitude range in C. finmarchicus to 4° in C. helgolandicus and C. hyperboreus). This shift corresponds to the population growth differential over the latitude and not an advection of individuals. For C. finmarchicus, C. glacialis, and C. hyperboreus, it also

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**Table 1. Explained deviance of Calanus spp. occurrence by each factor.**

<table>
<thead>
<tr>
<th></th>
<th>C. glacialis</th>
<th>C. hyperboreus</th>
<th>C. finmarchicus</th>
<th>C. helgolandicus</th>
</tr>
</thead>
<tbody>
<tr>
<td>PCI</td>
<td>0.27</td>
<td>0.16</td>
<td>0.16</td>
<td>4.15</td>
</tr>
<tr>
<td>PCI + diatoms + dinoflagellates</td>
<td>0.51</td>
<td>1.41</td>
<td>2.41</td>
<td>6.41</td>
</tr>
<tr>
<td>SST</td>
<td>26.3</td>
<td>17.7</td>
<td>11.6</td>
<td>10.0</td>
</tr>
<tr>
<td>Salinity</td>
<td>19.4</td>
<td>10.7</td>
<td>11.4</td>
<td>2.05</td>
</tr>
<tr>
<td>Bathymetry</td>
<td>1.06</td>
<td>3.59</td>
<td>4.72</td>
<td>15.7</td>
</tr>
<tr>
<td>Vertical velocity</td>
<td>0.53</td>
<td>1.32</td>
<td>1.09</td>
<td>5.47</td>
</tr>
<tr>
<td>Spatial terms (Lat:Long)</td>
<td>35.6</td>
<td>23.1</td>
<td>26.3</td>
<td>39.0</td>
</tr>
<tr>
<td>Month</td>
<td>3.78</td>
<td>19.3</td>
<td>3.91</td>
<td>0.55</td>
</tr>
<tr>
<td>Year</td>
<td>4.87</td>
<td>0.75</td>
<td>1.66</td>
<td>2.74</td>
</tr>
</tbody>
</table>
may correspond to the ascent of the overwintering population at the end of the diapause (Heath et al., 2004) rather than to a shift in the distribution of individuals remaining in surface during winter (the CPR only samples the surface layer). The gravity centre index used for Calanus spp. showed seasonal patterns which are consistent with the annual peaks reported for those taxa at different latitudes by other authors (Planque and Fromentin, 1996).

**Temporal analysis**

Population gravity centre indices throughout the years (Figure 7, Table 3) permitted to infer the following trends for each species according to the comparison between models and observed data. For *C. glacialis*, all models and observed (presence/absence) data showed a slight shift to the South (Figure 7a and c). This species presented relatively low occurrence in the data (i.e. *C. glacialis* was present in 5023 samples within the entire spatial domain and time-series, absent during 9 years) compared with other species (e.g. *C. finmarchicus* recorded in 105 598 samples in all years). This species has its main geographic distribution at Arctic and Subarctic regions; hence, enlarging the domain area of study beyond 65° is needed to confirm this result. For *C. hyperboreus*, observed data and the model based on the spatial and temporal terms indicate a shift to the South (Figure 7b and f). The combined model and the SST model showed no significant shift (Figure 7b). This means that species distribution probably shifted slightly to the Equator, while its habitat suitability was not expected to shift. This species, which presented relatively low occurrence in the data (present in 3853 samples, absent during 4 years), has its main geographic distribution in the Arctic and Subarctic regions; hence, enlarging the domain area of study beyond 65° is needed to confirm this result. For *C. finmarchicus*, all models showed poleward shift (Figure 7c and g). This means that species populations and its habitat suitability shifted poleward; hence, we can infer that population shift can be associated with sea warming. In particular, the spatial and temporal model indicates a population shift rate of 0.0073° latitude per year (8.1 km per decade) for the overall North Atlantic, and a slightly higher for the Northeast Atlantic (longitude between 30°W and 15°E; 16.5 km per decade) (Figure 7c). On the contrary, observed data showed that the gravity centre has a tendency to shift to the South (Figure 7g). This southward shift is due to the latitudinal decreasing trend in the sampling frequency (Figure 3b, Supplementary SI2), particularly north of 64° Latitude in the Northeastern Atlantic, in recent years, see Supplementary SI2. For *C. helgolandicus*, habitat suitability based on the SST model showed poleward shift since the 1970s; the combined model showed a similar result but the shift rate is less and starts from the 1980s (Figure 7d). On the contrary, the model based on spatial and temporal terms did not show a poleward shift. Observed data of *C. helgolandicus* showed slight southward shift for the presence/absence data, and no shift considering abundance data (Figure 7h).

**Table 2. Combined GAMs.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Variables selected</th>
<th>EDF</th>
<th>p-value</th>
<th>Overall explained deviance (%)</th>
<th>AUC (model with all observations/mean kfold cross-validation)</th>
<th>Accuracy (model with all observations/mean kfold cross-validation) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. glacialis</em></td>
<td>Year, SST, Salinity, Longitude, Month</td>
<td>3.979</td>
<td>&lt;1.10^-15</td>
<td>42.6</td>
<td>0.888/0.774</td>
<td>89.1/78.2</td>
</tr>
<tr>
<td><em>C. finmarchicus</em></td>
<td>Year, SST, Longitude, Lat, Month</td>
<td>3.940</td>
<td>&lt;1.10^-15</td>
<td>34.4</td>
<td>0.778/0.778</td>
<td>79.8/79.8</td>
</tr>
<tr>
<td><em>C. hyperboreus</em></td>
<td>Year, SST, Longitude, Lat, Month</td>
<td>2.759</td>
<td>&lt;1.10^-15</td>
<td>46.0</td>
<td>0.889/0.717</td>
<td>90.5/72.2</td>
</tr>
<tr>
<td><em>C. helgolandicus</em></td>
<td>Year, SST, Longitude, Lat, Month</td>
<td>3.988</td>
<td>&lt;1.10^-15</td>
<td>41.2</td>
<td>0.819/0.798</td>
<td>80.8/79.7</td>
</tr>
</tbody>
</table>

Variables entered: Year, month, longitude, latitude, SST, salinity, bathymetry, vertical velocity. EDF, Estimated Degrees of Freedom. Thresholds for the conversion of probability of species presence to either the presence or the absence in model validation: 0.05 (*C. glacialis*), 0.60 (*C. finmarchicus*), 0.03 (*C. hyperboreus*), and 0.30 (*C. helgolandicus*).
Overall, this means that species population probably did not shift poleward, and only its habitat suitability is shifted by sea warming.

**Discussion and conclusion**

GAMs for the four *Calanus* spp. in the North Atlantic have been built to analyse species distribution shifts between 1959 and 2004. GAMs were previously used to investigate the influence of environmental factors on plankton standing stock in the North Sea (Llope et al., 2009, 2012). Concerning the species habitat suitability, the limitation of distance-based habitat models used in previous works (e.g. Helaouet and Beaugrand, 2007, 2009; Beaugrand et al., 2008; Helaouet et al., 2011; Reygondeau and Beaugrand, 2011) to describe the asymmetry of ecological niche has been well solved by GAMs, which are usually more accurate according to model comparison studies (e.g. Elith et al., 2006). The models combining environmental and spatial factors have been validated using independent datasets and their reliability measure indicate moderate (72% for *C. hyperboreus*) to high accuracy performance (78–79% for *C. finmarchicus*, *C. glacialis*, and *C. helgolandicus*). The reliability of our data reconstruction models and the gravity centres used here, encompassing the overall population in the study area, might improve previous estimates of shift rates based only on observed data (e.g. Beaugrand et al., 2002).

Among the four analysed species, only *C. finmarchicus* showed a consistent poleward shift during the 1959–2004 period, as shown by all three models. This suggests that *C. finmarchicus* populations shifted poleward as a consequence of sea warming, since the SST model (i.e. habitat suitability) is consistent with the model with spatial and temporal terms (i.e. population data reconstruction; see maps in Supplementary SI3). This poleward shift is, overall, in agreement with previous works (see a review in Richardson, 2008). However, the rate of northward movement detected in *C. finmarchicus* (8.1 km per decade for the overall North Atlantic, 16.5 per decade for the Northeast Atlantic) is substantially lower than the change in distribution indicated for zooplankton assemblages by previous works for the Northeast Atlantic (260 km per decade for...
the northward extension of zooplankton assemblages 14 species including the four Calanus spp. analysed here; Beaugrand et al., 2002). The main differences between those studies are the taxa assemblage analysed, the statistic considered (distribution limits vs. geographic centres), and the model algorithm used. The gravity centre considered here is more reliable to capture overall population movement, since distribution limits may also change because overall increase in population abundance. The rate estimate here for C. finmarchicus is still higher than that reported for terrestrial species based on a study of 99 species of birds, butterflies, and plants (6.1 km per decade, Parmesan and Yohe, 2003) but within that of rattlesnakes (4.3–24.2 km per decade, Lawing and Polly, 2011). On the contrary, the population centre gravity in the observed data of C. finmarchicus showed a southward shift. This is most likely due to the lower sampling frequency at latitudes >64°N after the early-1980s (Figure 3b), as shown by the long-term mean latitude of sampling frequency (Supplementary SI2a and b); indeed, the Norwegian Sea, which is a core area of distribution for C. finmarchicus in the Northeast Atlantic, was poorly sampled between 1981 and 2004. Therefore, our data reconstruction modeling approach, which is supported by high model accuracy, shows its power in detecting latitudinal shifts even when observations are lacking due to discontinuous sampling.

Habitat suitability of C. helgolandicus based on SST showed poleward shift since 1970s. On the contrary, the model based on spatial and temporal terms did not show poleward shift, but an expansion of the overall population in the North Sea, Atlantic margin, and central N Atlantic since the 1970s (as shown by the predicted maps in Figure 7d and by the increasing variance of the gravity centre not shown here for brevity). This means that C. helgolandicus population did not shift poleward, although its habitat suitability changed probably as a result of sea warming. The causes of

Figure 6. Latitudinal shift of the population gravity centre during seasonal cycle (average for the overall 1959–2004 period; combined model). See text for explanation.

Figure 7. Shift in latitude of the gravity centre of Calanus spp. population habitat suitability models (a–d) and of the observed annual average (e–h), according to abundance and the presence/absence data. See estimations of trends (and their statistical significance) in Table 3.
Table 3. Latitudinal shifts (° year⁻¹) for each species and according to observed data and models between 1959 and 2004 in the North Atlantic.

<table>
<thead>
<tr>
<th>Species</th>
<th>Trend</th>
<th>p-value</th>
<th>Trend</th>
<th>p-value</th>
<th>Trend</th>
<th>p-value</th>
<th>Trend</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. glacialis</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed data (Pres/Abs)</td>
<td>-0.0386</td>
<td>0.0369</td>
<td>-0.1194</td>
<td>0.0006</td>
<td>-0.0641</td>
<td>4.5e-06</td>
<td>-0.0304</td>
<td>0.0042</td>
</tr>
<tr>
<td>Observed data (abundance)</td>
<td>-0.0174</td>
<td>0.3570</td>
<td>-0.0079</td>
<td>0.0252</td>
<td>-0.0453</td>
<td>0.0296</td>
<td>0.0119</td>
<td>0.6470</td>
</tr>
<tr>
<td>SST model</td>
<td>-0.0077</td>
<td>0.1787</td>
<td>-0.0024</td>
<td>0.2770</td>
<td>0.0086</td>
<td>1.0e-09</td>
<td>0.0119</td>
<td>0.0002</td>
</tr>
<tr>
<td>Spatial and temporal model</td>
<td>-0.0143</td>
<td>0.0136</td>
<td>-0.0044</td>
<td>&lt;2e-16</td>
<td>0.0073</td>
<td>&lt;2e-16</td>
<td>-0.0019</td>
<td>1.2e-06</td>
</tr>
<tr>
<td>Combined model</td>
<td>-0.0079</td>
<td>0.0049</td>
<td>-0.0020</td>
<td>0.5350</td>
<td>0.0123</td>
<td>&lt;2e-16</td>
<td>0.0029</td>
<td>0.0261</td>
</tr>
<tr>
<td>C. hyperboreus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. finmarchicus</td>
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<tr>
<td>C. helgolandicus</td>
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</table>

C. helgolandicus population expansion in all directions, including southward, are still unclear; one could hypothesize that it could be partially related to the general increase in phytoplankton biomass observed since the mid-1980s in the Northeast Atlantic (Raitos et al., 2005; McQuatters-Gollop et al., 2011). This is supported by the fact that the CPR phytoplankton indices explained C. helgolandicus occurrence in a larger extent than for the other three species (Table 1). The expansion of C. helgolandicus includes its northern distribution limit in the North Sea where it has replaced C. finmarchicus since the 1990s, which has been interpreted as a result of warming of this region (Richardson, 2008). Changes in abundance are more difficult to attribute to global warming than are shifts in distribution or phenology (Richardson, 2008). Our approach helps to disentangle shifts in species distribution and shifts in their habitats, reconstructing species expected occurrence even when observations are not available.

Southward population movement of the Arctic species (C. glacialis and C. hyperboreus) that have their main geographic centre at NW Atlantic is in agreement with previous works focused on the NW Atlantic (see Arctic and Subarctic assemblages in Beaugrand et al., 2002, and C. hyperboreus in Johns et al., 2001). The southward shift of these two species would respond to cool water penetrating southward in the NW Atlantic (Richardson, 2008), in particular in the Scotian and Newfoundland shelf regions influenced by the outflow of freshwater from the Arctic (Head and Pepin, 2010; Licandro et al., 2011). The spatial difference of SST between cold (1969–1979) and warm (1998–2004) periods (Figure 2b) showed that warming in the NW Atlantic (Labrador Sea) was more heterogeneous than in the NE Atlantic with three hotspots of warming and a region of cooling. This pattern could be related to the observed trend of the North Atlantic Oscillation (NAO) index towards positive values (Beaugrand et al., 2002) that result in warmer winters in the NE Atlantic and colder winters in the NW Atlantic (Hurrell, 1995) and might explain why C. glacialis and C. hyperboreus are showing southward shift. On the other hand, these two Arctic species were less frequent in the time-series (9 and 4 years without any presence for C. glacialis and C. hyperboreus, respectively) as their main geographic distribution is usually in Arctic and Subarctic regions, out of the area sampled by the CPR; hence, enlarging the domain area of study beyond 65° is needed to confirm these results.

Latitudinal shift of species is not the only potential response to ocean warming. Marine fish and invertebrates, for instance, can also respond to warming migrating to deeper waters (Cheung et al., 2013), similar to terrestrial species shifting their distribution to higher elevations within mountains (Engler et al., 2011). Using electronic tagging, Neat and Righton (2007) found that cod moved to cooler water at greater depths. The limitations of our data based uniquely on surface sampling (Jónasdóttir and Koski, 2011) preclude analysing whether there is also a shift towards deeper waters. In particular, Williams (1985) and Jónasdóttir and Koski (2011) observed that when C. helgolandicus and C. finmarchicus co-occur, the latter preferred colder deeper waters remaining reproductively active, while the former stayed in the warmer surface waters. In C. glacialis, Niehoff and Hirche (2005) found that temperature increase in the surface layer apparently triggered the descent of the females to lower depths and the arrest of their reproductive activity. In Neocalanus plumchrus, the timing of the annual maximum peak biomass has shifted 60 d earlier in warmer than in cold years over the past 50 years (Mackas et al., 1998). Such phenological change is probably a consequence of both increased survivorship of early cohorts and increase in physiological rates such as egg hatching, reproductive, and growth rate (Richardson, 2008). According to the study by Helaouet and Beaugrand (2009), the application of the ecological niche theory predicts that for northern hemisphere species, warming should produce increased survivorship in the northern (i.e. at cooler waters) population side in respect with its optimal niche, while it will diminish survivorship at the southern (i.e. at warmer waters) population side. Similarly, for competing species warming should produce increased competitive advantage four southern species with respect to northern species in overlapping areas. These two processes should cause latitudinal shift of the overall species distribution, thus, keeping pace with the shift of their suitable habitats. If vertical migration plays also a role in the climate response, even assuming that Calanus spp. could remain deeper ingesting an adequate ration of food, a drop in overall occurrence frequency at the two (northern-southern) sides of optimal (realized) niche should be observed in CPR surface-based data, which is not the case for C. helgolandicus according to our results.

Among the environmental factors, SST is, in general, the one explaining most of the variance of species occurrence in the four Calanus spp. (especially in C. glacialis), in agreement with previous works (Beaugrand et al., 2013) and the view of temperature as the most broadly influential factor controlling biological processes (Brown et al., 2004). Other environmental factors that could be taken into account in future studies to improve trend analysis and habitat suitability models are horizontal currents, food resources, and suitability of the overwintering habitat (Irigoien, 2004). As autonomous motility of copepods is spatially limited when compared with passive movement triggered by ocean currents, dispersal by this means might influence the probability of occurrence of a species at a given location from month to month. Phytoplankton indices used here and Calanus occurrence were poorly related according to our modelling approach as in previous attempts (e.g. Reygondeau and Beaugrand, 2011), either because those indices represents only part of the food available or because food is not a limiting factor. Phytoplankton is a key food source for calanoid species (Moller
et al., 2012); hence, other phytoplankton indices (satellite-derived primary production) or other ways of modelling food resources in the habitat suitability model should be explored in the future. Further, factors affecting overwintering survival such as winter mixing depth or distribution of predators might also play a role in the final distribution (Irigoin, 2004).

Another relevant finding of this study is that environmental variables accounted for 17–31% of species occurrence, which is less than did spatial and temporal terms (33–45%) in all Calanus spp., with high covariation among both types of factors. This means that space and seasonality are key to describe the pelagic distribution of copepods. Also, since spatial and temporal terms can be partially a proxy of dispersal constrains, our results are in line with a balanced view between the importance of the role of dispersal limitation and of niche partitioning on the plankton community structure (see for instance, Irigoien et al., 2011, for zooplankton and Chust et al., 2013, for phytoplankton).

Since species habitat models developed here have high accuracy, according to model evaluation using independent datasets, they have also the potential to be applied to future climate change scenarios to assess warming impacts on zooplankton and to assess the implications of changes at this trophic level vs. top predators such as fish and cetaceans. As we have seen, warming can modify the distribution of marine organisms, which in turn, it can be propagated through the upper trophic levels. In a context of rapid alteration of marine ecosystems throughout the world (Pauly et al., 1998), future projections of ocean productivity, based on habitat species distribution, are needed for a detailed assessment of ocean health and benefits and for achieving or maintaining the good environmental status of the North Atlantic (see for instance, the environmental status defined by the Marine Strategy Framework Directive, MSFD; European Commission, 2008).

In summary, our findings show that among the four Calanus spp. analysed in the North Atlantic during the 1959–2004 period, only C. finmarchicus had a consistent poleward shift estimated in 8.1 km per decade (16.5 km per decade for the Northeast Atlantic), triggered by sea warming, which is lower than previous works restricted to the Northeast Atlantic and considering zooplankton assemblages. Because of the sampling limitation of the CPR survey in the northern regions, it is not possible to clarify whether C. finmarchicus global gravity centre has displaced to the North or rather its southern distribution has retracted. Our model is highly accurate (80%), which has been validated by a subset of observational data. It shows its power in detecting latitudinal shifts even when changes in the sampling frequency may not ensure an adequate coverage of a region. On the contrary, C. helgolandicus population gravity centre did not shift poleward according to the results, although its northern distribution limit in the North Sea has shifted northward. Calanus helgolandicus is expanding in all directions probably influenced by multiple factors (e.g. phytoplankton increase, warming, their own population dynamics, biotic interactions, environmental variability). Calanus glacialis and C. hyperboreaea based on the CPR sampling, present the geographic centres of their populations mainly in the NW Atlantic, showed a slight southward shift, probably responding to cool water penetrating south in the Labrador Current and the heterogeneity in the warming at NW Atlantic. Despite of the limitations of CPR data restricted to surface sampling, the long and spatially extensive biological dataset, together with species occurrence models based on a wide range of factors (climate, spatio-temporal) and tested in a combined and separate manner, has the potential to detect and accurately quantify latitudinal shifts and suggests potential causes.

**Supplementary data**

Supplementary material is available at the ICESJMS online version of the manuscript.

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**References**


Are Calanus spp. shifting poleward in the North Atlantic? 253


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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, sipholophores, 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 (Zsp) 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.
zoo plankton or plays an important role in structuring the zoo plankton 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; Li et al., 2009, 2012b; Stegert et al., 2012; Maar et al., 2013) or individual-based models (IBMs; e.g., Hjollo 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 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 Irgoien, 2004; Zaraux et al., 2008; Irgoien et al., 2009) as well as abundance and size distribution (Nogueira et al., 2004; Sourisseau and Carlotti, 2006; Irgoien 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 Irgoien, 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 poutassou), European hake (Merluccius merluccius), and anglerfish (Lophius piscatorius and Lophius budgessa) 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, Nassale 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 complex structure, where the microbial loop takes over and mesozooplankton on forage fish. Extensive reviews of the resident zooplankton and fish. 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 (Ammodites 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 temporarily 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; Pitosi 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; Pitosi 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 (Rydelberg 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 (Rydelberg 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* (Kiørboe 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 (Tönnessen and Tiselius, 2005; Tönnessen 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 (Tönnessen and Tiselius, 2005; Tönnessen 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$^{-1}$ (Kiørboe and Nielsen, 1994). Copepod egg mortality was particularly high during the spring bloom, probably due to cannibalism and low hatching success as shown in Kiørboe 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 copepod 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
zoooplankton species and their predators. The main fish species preying on open sea zoooplankton are the clupeids sprat and herring for which copepods form the major food source (Arthenius 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 (Vihervuoto 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 zoooplankton 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 norwe-
com.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 interannual 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 phytoplanクト 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 dominate 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. carnatus, 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 (Verhey and Richardson, 1998; Verhey 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 (Verhey and Richardson, 1998). The latter can induce (i) an increase in phytoplankton biomass due to enrichment of nutrients, (ii) advectons 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 (Verhey, 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 (Verhey and Richardson, 1998; Verhey 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 (Verhey 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 (Hjelto et al., 2012; Ume 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 ($\mu$), 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 \( \mu_p \) for weight (size) \( z_i \) at time \( t \) as:

\[
\mu_p(z_i, t) = \int_{z_i}^{\text{max}} p(z_i, z', t) B(z', t) \, dz,
\]

where \( B(z', t) \) is the biomass in the predator size group \( z' \) and \( p \) the predation rate in the size group \( z_i \) 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 where 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 \( \mu \) in a size class \( z_i \) 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 \( \text{d} \mu(z_i, t) = gS \). 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 pallasi) 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 eCO Systems Exploitation) simulates individual fish interacting via an opportunistic predation process (Shin and Curry, 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 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; Hjollo et al., 2012; Utne and Huse, 2012). In contrast to the OSMOSE example, zooplankton is not part of the biogeochemical 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 way. 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 tropic 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, mesozooplankton 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 changes 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 of 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 (Zinc) of the biomass is subjected to intra-guild predation and that the rest (1 – Zinc) 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 Zinc 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 Ibanez, 2000). In contrast, in the systems where zooplankton experienced 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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Daytime depth and thermal habitat of two sympatric krill species in response to surface salinity variability in the Gulf of St Lawrence, eastern Canada

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We describe the response of acoustically determined weighted mean depth (WMD) of two sympatric species of krill, Thysanoessa raschii and Meganyctiphanes norvegica, to variations in surface salinity during summer in the Gulf of St Lawrence. In this coastal system, non-living particulates and CDOM carried by the freshwater run-off of the St Lawrence River and several large rivers have a strong impact on turbidity and light attenuance in the surface layer. The WMD of T. raschii and M. norvegica were significantly and positively related to surface salinity. However, M. norvegica was found deeper and in warmer water than T. raschii, and the latter had a steeper response to surface salinity. The species-specific relationships between daytime WMD and surface salinity enabled us to estimate both species regional and interannual variations in summertime temperature habitat during a 21-year period (1991–2011). The variability in daytime WMD resulted in significant inter- and intraspecific differences in the temperature experienced by adult krill that may impact development, growth, and reproduction. Our study illustrated the importance of considering species-specific responses to environmental forcing in coupled biophysical models that aim to explore the impacts of environmental variations on krill dynamics.

Keywords: Gulf of St Lawrence, krill, Meganyctiphanes norvegica, Thysanoessa raschii, vertical distribution.

Introduction

General patterns of diel vertical migration (DVM) by krill and other zooplankton species have been described for many decades (Russell, 1927; McLaren, 1963; Isaacs et al., 1974; Pearre, 1979). Classical DVM is an upwards swimming of individuals at dusk from a few hundred metres depth to feed in the surface layer at night and a subsequent downwards migration at dawn back to their daytime refuge (Mauchline, 1980; Pearre, 2003; Kaartvedt, 2010). DVM behaviour likely results from a trade-off between increased individual growth and reproductive output and increased visual predation risk within the food-rich surface layer (e.g. De Robertis, 2002). However, krill DVM remains plastic, responding to a variety of endogenous and exogenous factors (Kaartvedt, 2010). For example, krill can be found near the surface during the day or at depth at night, behaviours associated with reproductive behaviour (mating and spawning) and moulting, respectively (Nicol, 1986; Tarling et al., 1999). The timing and the duration of the different phases in krill DVM, as well as its vertical extent, interact with environmental gradients and impact the physiology and population dynamics of krill. The vertical extent of the DVM is of particular importance in systems presenting strong vertical gradients in temperature and currents (thermoclines and vertical shear; e.g. Batchelder et al., 2002).

The system formed by the Gulf of St Lawrence (GSL) and its lower estuary (SLE) is such an environment. It is characterized by strongly stratified physical conditions (salinity, temperature, and circulation) and important seasonal and interannual variations in physical forcing (Koutitonsky and Bugden, 1991; Saucier et al., 2003; Galbraith et al., 2012). A brackish surface layer (22–30 PSU, 0–30 m) influenced by the freshwater outflow...
from the St Lawrence River and other tributaries is separated from deep Atlantic waters (≥100 m, 4–5°C, 34–35 PSU) by a colder and fresher intermediate layer (CIL; negative minimum temperatures, 31–33 PSU) between ~30 and 100 m (Figure 1a; Koutitonsky and Bugden, 1991; Gilbert and Pettigrew, 1997; Galbraith, 2006). The St Lawrence River provides ~70% of the freshwater run-off, whereas the North Shore rivers combined (including the Saguenay) provide almost all the remainder. Owing to its high load of terrigenous material, the freshwater outflow from major tributaries controls spatial, seasonal, and interannual patterns in surface salinity and turbidity altogether (Le Fouest et al., 2006, 2010). The SLE and the northwest GSL (NWG) are more influenced by freshwater run-off than the eastern GSL (EG; Le Fouest et al., 2010; Galbraith et al., 2012), generating a clear horizontal gradient in the surface salinity (Figure 1b). Surface salinity remains significantly lower in the GSL than in the Northwestern Atlantic outside the GSL. Two krill species, _Meganyctiphanes norvegica_ and _Thysanoessa raschii_, overwhelmingly dominate the krill population in the SLE and NWG (Berkes, 1976; Simard et al., 1986a, b; Harvey and Devine, 2009). Although both _M. norvegica_ and _T. raschii_ migrate to the surface layer at night to feed (Berkes, 1976; Simard et al., 1986b; Sourisseau et al., 2008), _M. norvegica_ shows a deeper daytime vertical distribution than _T. raschii_ (up to 100 m deeper according to Berkes, 1976). The daytime depth difference between both species implies that _T. raschii_ could be more associated with the CIL, hence exposed to colder temperatures than _M. norvegica_. The daytime depth would determine each species’ thermal habitat during a significant portion of its diel cycle during the growth season. Given the effect of temperature on krill biology (e.g. Iguchi and Ikeda, 2004) and the temperature difference of up to 5°C between the core of the CIL and the Atlantic waters below, an accurate determination of species-specific daytime weighted mean depth (WMD) is important for the study of the impacts of environmental variability on krill production in the GSL.

The factors involved in the selection by krill of its daytime depth are known to some extent. The most important factor seems to be a critical isolume associated with negative phototaxis (Kaartvedt, 2010). Light irradiance serves as a proxy for the risk of visual predation for krill. This effect has been observed in _M. norvegica_, which actively adjusts its vertical position to track a specific isolume over a diel cycle or in response to a local alteration in light penetration (Onsrud and Kaartvedt, 1998; Frank and Widder, 2002). Although temperature is a major environmental forcing factor in most aspects of krill biology, it does not appear to be a key factor in its depth selection (Cohen and Forward, 2009; Kaartvedt, 2010). The eurythermal _M. norvegica_ in particular is found across large seasonal and geographical temperature ranges and seems to perform DVM in waters of widely different temperatures, from the boreal North Atlantic to the Mediterranean Sea. However, our understanding of the mechanisms involved in the regulation of DVM in general and the determination of daytime depth in particular remains limited for _M. norvegica_, and even more limited for _T. raschii_. The current lack of understanding of factors controlling DVM hampers the formulation of mechanistic functions in coupled biophysical models that are necessary to study spatio-temporal variations in distribution and growth of krill species (e.g. Burrows and Tarling, 2004; Atkinson et al., 2006; Cresswell et al., 2007, 2009). In particular, the assumption of a fixed daytime depth in zooplankton modelling (e.g. Sourisseau et al., 2006; Maps et al., 2011) may have a significant impact on population dynamics modelling (Batchelder et al., 2002).

Hence, the first objective of our study was to describe the response of daytime WMD of _M. norvegica_ and _T. raschii_ to variations in two environmental parameters during the productive season: surface salinity and the depth of the lower limit of the CIL. WMDs were estimated by data collected with an acoustic multifrequency system during surveys of krill biomass from Fisheries and Oceans Canada (DFO). Surface salinity (average 0–10 m) is tightly correlated with turbidity and surface light irradiance attenuation in the case II waters from the SLE and NWG (Le Fouest et al., 2010). Surface salinity is more often measured than turbidity or light profiles and may be used as a proxy for _in situ_ irradiance to predict the association of WMD with thermal habitat. As _M. norvegica_ could be at the lower threshold of its thermal tolerance within the CIL, the depth of the lower limit of the CIL (defined as the 1°C isotherm) was another independent variable considered. This variable allowed the testing of whether species-specific daytime WMD is influenced by the
thermal preferences of the boreal *T. raschii* and the eurythermal *M. norvegica*. Our second objective was to quantify the impact of variable species-specific daytime WMD on the thermal habitat experienced by each species over the last two decades in different regions of the GSL. We discuss our results in the context of *M. norvegica* and *T. raschii* physiology and production in the GSL, and about numerical modelling in the GSL.

**Material and methods**

**Krill sampling and vertical distribution**

Species-specific krill vertical distribution was determined in summer 2008 and 2009 with a Simrad EK60 multifrequency echosounder (38, 70, 120, and 200 kHz) during DFO’s spatially stratified surveys aimed at estimating krill and pelagic fish biomass in the SLE and NWG (Figure 2a). Sampling was performed during daylight, approximately from 6 a.m. to 6 p.m. and concentrated around noon. The stratified sampling strategy was employed to concentrate effort in the shelf and slope areas (<180 m) where krill was found to aggregate based on exploratory acoustic surveys, while dedicating a lesser sampling effort in the deeper waters (>180 m) of the Laurentian Channel. The multifrequency approach, similar to others recently developed and applied in other regions (e.g. De Robertis et al., 2010), was used to acoustically identify *T. raschii* and *M. norvegica* to species based on intrinsic differences in their frequency responses, due mainly to their non-overlapping length distribution. Here, we briefly outline the acoustic sampling and data processing procedures detailed in McQuinn et al. (in press). Scattering layers were first averaged in 2 × 25 m (vertical × horizontal) bins of *s* backscatter at 38, 120, and 200 kHz for subsequent classification into four classes from their frequency response: swimbladdered fish (principally herring and capelin) and non-swimbladdered fish (principally sand lance and mackerel), *Thysanoessa* spp. (overwhelmingly *T. raschii* in the ESL–GSL, Berkes, 1976), *M. norvegica*, and a mixed class of *T. raschii* and *M. norvegica*. Since we did not acoustically distinguish between *M. norvegica* and mysids, the classification was applied to the upper 220 m to avoid the usually deeper mysid scattering layer (Harvey et al., 2009). High abundance of the large bodied copepod *Calanus hyperboreus* and *C. finmarchicus* are also common in the region (Plourde et al., 2003), although at densities rarely exceeding 2–3 g m$^{-3}$ above 220 m, well below the −80-dB threshold applied for krill detection.

We considered only data classified in the mutually exclusive *T. raschii* or *M. norvegica* classes for our subsequent analyses. The mixed class represented always less than 5% of the biomass. The daytime WMD (Bollens and Frost, 1989) of *T. raschii* or *M. norvegica* biomass was estimated from the integration of the species-classified echoes at 120 kHz with a 2-m vertical resolution averaged according to depth strata and in the proximity of 42 CTD casts to obtain salinity and temperature profiles that could describe the oceanographic environment (Figure 2a). Only the data showing that the topography did not strongly constrain the krill vertical distribution were selected for further analysis.

**Environmental variables**

Three environmental variables were extracted from 42 CTD casts made near the acoustic density data: (i) the salinity profile and the corresponding surface mixed layer salinity averaged between 0 and 10 m (S$_{0-10m}$), (ii) the depth of the lower limit of the CIL defined as the deeper 1°C isotherm (Z$_{CIL}$), and (iii) the temperature at the depth of the WMD of each krill species. In situ light irradiance was not measured on a routine basis during these surveys. Hence, we estimated the light irradiance ($I_z$) as a function of depth $z$ from the Beer–Lambert’s law:

$$I_z = I_0 \times \exp(-(k_w + k_d) \times z) \quad \text{in \ \mu E \ in \ m^{-2} \ s^{-1}} \quad (1)$$

where $I_0$ is the visible light available at the surface of water, $k_w$ the diffuse attenuation of light by pure seawater (0.04 m$^{-1}$), and $k_d$ the attenuation coefficient of non-chlorophyllous matter. $I_0$ came from the four times the daily mean of the visible beam downwards solar flux model output of the NCEP/NCAR Reanalysis 1 (accessed December 2012; http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.surfaceflux.html). We used the value the closest in space and time to our observations in the GSL. In the case II waters from the SLE and NWG, there is a highly significant relationship between the $k_d$ attenuation coefficient and the salinity (Le Fouest et al., 2006):

$$k_d = -0.0364 \times S + 1.1942 \quad (r^2 = 0.71), \quad \text{with} \quad 26 < S < 32 \quad (2)$$
We neglected the contribution of chlorophyll material to the total diffuse attenuation coefficient, since it is less than 20% during the summertime post-bloom conditions in the western GSL (Le Fouest et al., 2010). We used a simple forward numerical iterative scheme to compute the light profiles.

Daytime WMD was regressed with \( S_{0-10m} \) or to \( Z_{1C} \) as potential explanatory variables. Temperature at the daytime WMD was used to describe the thermal habitat of krill. Only CTD stations deeper than the predicted daytime WMD were included (\( n = 3745; \text{Figure } 2b \)).

To characterize the interspecific, interannual, and regional variability of the daytime thermal habitat of adult krill, we extended the analysis over a 21-year period (1991–2011) using a CTD dataset collected by DFO that covered the whole GSL in summer. Temperatures at the specific daytime WMDs predicted by the significant relationships with environmental variables found here were averaged for each of the 21 years and over three oceanographic regions of the GSL: the SLE, NWG, and EG (Figure 2b). Finally, to assess the physiological impact of the fixed daytime depth assumption in modelling studies, we also compared the temperatures observed at the WMD to temperatures at a fixed depth of 150 m.

**Results**

**Krill daytime vertical distribution in the SLE and NWG**

*Meganyctiphanes norvegica* and *T. raschii* vertical distribution in August 2009 is representative of the vertical distribution profiles observed and used for subsequent analysis in this study (Figure 3). In the slope area (bottom depth of 180 m) located along the south shore of the SLE (strata 2C in Figure 2a), the bulk of *T. raschii* population was centred at 90 m, whereas the density of *M. norvegica* peaked at 110 m (Figure 3a). In strata 1A located on the slope along the north coast of the NWG (bottom depth of 200 m, Figure 2a), both krill species were located much deeper, with the maximum density of *T. raschii* and *M. norvegica* observed at 150 and 180 m, respectively (Figure 3b). This profile from strata 1A was the one where the *M. norvegica* WMD was the closest to the bottom. In both instances, only a proportion of less than 5% of the krill biomass was attributed to the undetermined mixed class.

Together, all the observed daytime WMD spanned a depth range of almost 100 m for each krill species (Figure 4). *Meganyctiphanes norvegica* WMD was located between 108 and 189 m (range = 81 m), whereas *T. raschii* WMD was spread a little more from 65 to 155 m (range = 90 m; Figure 4a). The average daytime WMD was significantly deeper for *M. norvegica* (145 ± 2.7 m s.e.) than for *T. raschii* (115 ± 3.8 m s.e.; paired \( t \)-test, \( p < 0.0001 \)). This translated into significantly different species-specific thermal habitats (Figure 4b). The total range of temperature at the WMD was ~4°C in both species, although *M. norvegica* WMD were observed completely below the CIL (between 1.3 and 4.2°C), and about one-third of *T. raschii* observations were located inside the CIL (total range of –0.7 to 3.4°C). *Thysanoessa raschii* daytime WMD were found in waters on average 1.15°C colder than *M. norvegica*.

**Krill daytime WMD vs. environmental conditions in the SLE and NWG**

Daytime WMD of both krill species were not related to the depth of the bottom of the CIL (Figure 5a). Daytime WMD resulted in low ambient light levels, with no detectable correlation between both variable (Figure 5b). The absence of relationships is in accordance with the hypothesis that the daytime WMD of krill is a behavioural response to ambient light level. The species-specific means in light irradiance at WMD (assumed to be preferred light levels) were significantly different (\( t \)-test, \( p < 0.001 \)), being three times higher for *T. raschii* than for *M. norvegica*. Daytime WMD of *T. raschii* and *M. norvegica* both showed a significant linear positive relationship with \( S_{0-10m} \) (\( r^2 = 0.74 \) and \( r^2 = 0.57 \), respectively), indicating that the surface layer turbidity associated with freshwater run-off (0.029 < \( k_p < 0.32 \text{ m}^{-1} \) for 26 < \( S_{0-10m} < 32 \text{ PSU} \)) was the primary factor regulating krill daytime WMD in the region during summer (Figure 6a). *Meganyctiphanes norvegica* and *T. raschii* were both observed higher in the water column at low \( S_{0-10m} \) and deeper at high \( S_{0-10m} \) but the slopes of the species-specific regressions were significantly different (analysis of covariance, \( p < 0.001 \)). Because of the general vertical temperature structure in the GSL (Figure 1a), the daytime thermal habitat of both krill species warmed up as \( S_{0-10m} \) increased and the daytime WMD fell further away from the CIL (Figure 6b).

**Impact of daytime WMD on krill thermal habitat in the GSL**

The species-specific relationships observed between daytime WMD and surface salinity predicted significantly different thermal habitats for each species as well as for populations from different regions of the GSL (Figure 7a), when applied to 21 years of summertime CTD profiles (Figure 2b). The eastward horizontal gradient in surface salinity (Figure 1b) predicted an eastward deepening of the WMD associated with a warming of the...
daytime thermal habitat of adult krill from both species as they are driven further away from the bottom of the CIL (Figure 7a).

However, the interspecific difference in the slopes of the linear regressions (Figure 6a) resulted in larger interspecific differences in thermal habitat in the SLE (average 1.06°C) than in the NWG or EG (both average at 0.88°C; Figure 7b). The comparison between temperatures at the predicted daytime WMD (TWMD) and temperatures at 150 m (T150m) revealed the impact of a fixed daytime depth approach when studying krill in the GSL (Figure 7c). The use of a fixed daytime depth resulted overall in significantly different biases in daytime temperature for T. raschii and M. norvegica [analysis of variance (ANOVA), p < 0.0001]. Temperatures at 150 m overestimated daytime temperatures for T. raschii (T150m - TWMD = 0.65°C), whereas they underestimated daytime temperatures for M. norvegica (T150m - TWMD = -0.24°C). Moreover, intraspecific biases in daytime temperature were significantly different among regions (ANOVA, p < 0.0001). For T. raschii, differences between T150m and TWMD were larger in the SLE (+1.2°C on average) and the NWG (+0.60°C) than in the EG (+0.06°C; Figure 7c). For M. norvegica, T150m underestimated TWMD in the EG (-0.73°C) and in the NWG (-0.25°C), whereas it slightly overestimated TWMD in the SLE (+0.25°C; Figure 7c). Intraspecific regional errors were equivalent to the interspecific errors in thermal habitats (average ~1°C). The spread of values in each boxplot represents interannual variability (within the 21 years of data) in the differences between T150m and TWMD. For T. raschii, the maximum absolute error using T150m is ~2°C, whereas it is close to 1°C for M. norvegica.

Discussion
Daytime vertical distribution of krill and environmental parameters
Our study demonstrated that of the two physical parameters tested (surface salinity and the depth of the bottom of the CIL), only surface salinity (S0-10m) was a predictor of daytime WMD for both krill species in the SLE and NWG in summer (Figure 4). Assuming that the penetration of light irradiance through the water column is the major control of krill vertical distribution during daytime, we explain the impact of surface salinity by the
Daytime depth and thermal habitat of two sympatric krill species

(white dots) according to surface salinity ($T. raschii$)

Figure 6. (a) Observed daytime WMD of adults $M. norvegica$ (black dots) and $T. raschii$ (white dots) according to surface salinity ($S_{0-10 m}$). Regression of $M. norvegica$: WMD = 7.5 x $S_{0-10 m}$ - 64, $r^2 = 0.57$; $T. raschii$ (dashed line): WMD = 11.4 x $S_{0-10 m}$ - 201, $r^2 = 0.74$. (b) Observed temperature at WMD of adults $M. norvegica$ (black dots) and $T. raschii$ (white dots) according to surface salinity ($S_{0-10 m}$). Note that the temperature scale is increasing down to respect the natural representation of the temperature profile. Regressions of $M. norvegica$: $T = 0.27 x S_{0-10 m} - 4.6$, $r^2 = 0.36$; $T. raschii$ (dashed line): $T = 0.51 x S_{0-10 m} - 12.3$, $r^2 = 0.51$. Dotted lines, 95% confidence interval of the mean.

particulate and dissolved terrigenous material associated with freshwater run-off that controls the variability in diffuse attenuation of light in the GSL system (Le Foust et al., 2006, 2010). Surface salinity was a proxy of the regional variations in light levels driven by seasonal and interannual variations in freshwater discharge in the system, a major driver of physical, optical, and biological conditions in the GSL system (Koutitsky and Bugden, 1991; Le Foust et al., 2006; Saucier et al., 2009). The use of surface salinity as the only proxy of the light environment of krill neglected the impact of other potential controls of the light level, such as phytoplankton concentration, cloud cover and seasonal variability in surface incident light or in the nature of the material load that affects light attenuation. However, surface salinity by itself explained the majority of the variance in the species-specific daytime WMD distribution. The strength of the species-specific relationships between surface salinity and daytime WMD also suggests that other potential controls not related to light played a minor role at the scale considered in our study. For example, hypoxia has been shown to limit $M. norvegica$ daytime depth (Kaartvedt, 2010), but the oxygen concentration threshold that would have an effect (7–10% O2 saturation) is much lower than the minimum observed in the GSL (c.a. 20% O2 saturation; Gilbert et al., 2005). The presence of predators is another potential factor influencing krill daytime distribution (Onsrud and Kaartvedt, 1998; Kaartvedt, 2010); however, data on this interaction are lacking in the GSL.

Our results also highlighted the important potential for plasticity in $M. norvegica$ and $T. raschii$ daytime WMD in response to regional, seasonal, and interannual variations in surface salinity in the GSL. Thysanoessa raschii and $M. norvegica$ had species-specific responses to the light attenuation variability associated with the surface salinity (Figure 4b). The consistently deeper WMD of $M. norvegica$ compared with $T. raschii$ was in accordance with previous observations from the SLE and GSL (Berkes, 1976; Harvey et al., 2009). While daytime WMD in both species responded in the same way to variations in surface salinity, the distance between $M. norvegica$ and $T. raschii$ increased with decreasing surface salinity (decreasing light level). The definitive mechanism behind these different behaviours remains elusive as it could involve several environmental and biological variables (Kaartvedt, 2010). A first likely cause is the exponential attenuation of light within the water column. It can lead to the different slopes in the linear fit of WMD to surface salinities, providing $T. raschii$ stops its downwards migration when it reaches a light threshold higher than $M. norvegica$ (Figure 5b). Species-specific responses to ambient light levels are likely. For instance, photosensitivity varies considerably among $M. norvegica$ individuals developing in environments of different turbidity and it is likely to be a trait showing phenotypic plasticity in response to regional conditions (Myslinsky et al., 2005). However, the validity of this hypothesis is difficult to assess given the current lack of knowledge of the photosensitivity of $T. raschii$ and of $M. norvegica$ in the GSL. For $M. norvegica$ specifically, it could be that the very cold temperatures in the CIL modulate $M. norvegica$ vertical distribution when low levels of light irradiance bring this population in contact with the CIL. In our observations, $M. norvegica$ WMDs are always found in temperatures higher than 1°C (Figure 4b). This pattern contrasts with $T. raschii$ that is often observed inside the CIL (Figure 4b). It could be that very low temperatures. However, the lack of a significant relationship between the depth of the bottom of the CIL and this species WMD (Figure 5a), as
well as the regular increase in temperature following the WMD (Figure 6b), does not seem to support this hypothesis. The role of size-dependent DVM amplitude may also be considered. The larger *M. norvegica* individuals would perform larger DVM than the smaller *T. raschii* (e.g., Bollens et al., 1992). Another mechanism is mutual exclusion, *T. raschii* possibly avoiding the larger and more carnivorous *M. norvegica* located deeper in the water column (Kaartvedt, 2010). But although the latter two hypotheses address the deeper distribution of *M. norvegica* relative to *T. raschii*, they cannot explain the difference in regression slopes between surface salinity and daytime WMD.

**Impacts of daytime thermal habitat on krill ecology**

Temperature has a major influence on zooplankton biology. However, estimating the impacts of temperature variability on krill biology and population dynamics is complicated by the distinct influences temperature exerts on metabolism-related processes and on development and maturation processes. Development and maturation are generally more sensitive to temperature change than metabolism (Forster and Hirst, 2012). Knowledge of the temperature sensitivity of *T. raschii* is very scarce, but the few *Q*\(_{10}\) coefficient measurements available for some *Thysanoessa* species and for *M. norvegica* in the GSL and elsewhere in the North Atlantic (Table 1) show an average *Q*\(_{10}\) of 2.3 for the intermoult period (IMP) and a lower average *Q*\(_{10}\) of 1.9 for respiration (reviewed in Spicer and Saborowski, 2010). These *Q*\(_{10}\) coefficients mean that a temperature change of 4°C, equivalent to the intraspecific daytime temperature range observed in this study, would result in substantial changes in development and metabolic rates (∼40 and 30%, respectively). Hence, the intraspecific regional and interannual variability in daytime thermal habitat could have a significant impact on krill biology in the GSL during summer.

Although sampling method and period allowed us to detect primarily adult krill, we will explore in this paragraph the potential metabolic impacts of variable thermal environments during krill ontogeny. Assuming that growth results from the integration of metabolic processes over the IMP, the difference in temperature sensitivities of growth and development implies that krill body size decreases as temperature increases (Forster and Hirst, 2012). A 4°C increase in daytime temperature that would persist during 12 h should result in a 20% shorter IMP not compensated for by a 15% increase in the anabolic rate. Hence, a testable hypothesis is a spatial gradient in the body size of adult krill that would follow the species-specific spatial gradient in daytime temperature predicted in the GSL during summer. However, observations pertaining to the role of environmental forcing on *in situ* krill growth are equivocal. *In situ*, IMP seems to respond essentially to temperature, while growth may relate more to food availability in a generally food-limited environment (Siegel and Nicol, 2000, and references therein; but see Saunders et al., 2007). In the GSL, in the SLE, NWG, and EG, (c) Distribution of the temperature difference between a fixed depth of 150 m and the predicted species-specific WMD in the SLE, NWG, and EG. For all panels, individual values are the average over the region and summer (June to August) of each year from 1991 to 2011. Boxes show the median and 25th–75th percentiles; whiskers the 10th–25th and 75th–90th percentiles; dots the outliers.

**Figure 7.** (a) Distribution of temperature at the daytime WMD of adults *T. raschii* and *M. norvegica* predicted according to surface salinity (*S*\(_{0–10m}\)) measurements from 1991 to 2011 in three regions of the GSL: SLE, NWG, and EG. Note that the temperature scale is increasing down to respect the natural representation of the temperature profile. (b) Distribution of temperature difference between *M. norvegica* and *T. raschii* at their predicted daytime WMD.
Table 1. Observed sensitivity to temperature ($Q_{10}$ coefficient) of respiration and IMP for *M. norvegica* and *Thysanoessa* sp. from the North Atlantic.

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<th>Meganymphenes norvegica</th>
<th>Thysanoessa sp.</th>
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<td>Cuzin-Roudy and Buchholz (1999) (Figure 3)</td>
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however, the characteristic negative eastwards gradient in phytoplankton production (observed: de Lafontaine *et al.*, 1991; modelled: Le Fouest *et al.*, 2010) would also tend to produce smaller individuals in the EG compared with the NWG and SLE.

Adult female body size has a significant positive allometric relationship with the number of eggs per clutch spawned (Cuzin-Roudy, 2000). Hence, smaller krill females should lay fewer eggs. However, egg production cycles are synchronized with moultin g cy cles and the spawning frequency results in similar lifetime fecundity for *M. norvegica* females inhabiting environments with contrasting temperature regimes, from the Mediterranean to the North Sea (Cuzin-Roudy, 2000). A more important impact of variable daytime temperature on the population dynamics of both krill species may then be linked to the associated change in the timing of moultin g and thus the timing of egg production. Tarling and Cuzin-Roudy (2003) showed that during the productive season the successive spawning events of the *M. norvegica* population from the Clyde Sea were synchronized. Successful recruitment then occurred only when phytoplankton concentration was sufficient for the development of the larvae, and less than half of the cohorts of eggs managed to recruit as juveniles.

**Implications for krill modelling**

A thorough examination of historical datasets and further *in situ* observations are required to determine the relative impact of daytime vertical temperature distribution on the krill biology in the GSL system. Numerical modelling is also an efficient and necessary tool for disentangling environmental effects on growth and development of krill. For example, Wiedenmann *et al.* (2008) explored complex synergistic effects of temperature and food in a modelling study that predicted contrasting responses of *Euphausia superba* growth to warming in two regions of the Antarctic. In the GSL, a complex response to global warming is also expected. The effect of global warming on freshwater run-off is difficult to predict as the sign of future trends vary depending on the climate model used, on the warming scenarios used to force a particular model, as well as on the watershed considered (e.g. Angel and Kunkel, 2010; Chen *et al.*, 2011). But whatever the sign of the change may be, it will most likely affect the turbidity and daytime depth distribution of the krill, according to our results. Our results demonstrate the importance of identifying relationships between biological parameters and variable environmental conditions at the species level. We provide the first of such a relationship between the daytime WMD of *T. raschii* and *M. norvegica* to seasonal, interannual, and spatial variations in the light level controlled by freshwater run-off, a key driver of the circulation, the physical, and the biological environments in the GSL (Koutitonsky and Bugden, 1991; Saucier *et al.*, 2003; Le Fouest *et al.*, 2010). Population-based biophysical coupled models necessary to identify and describe the mechanisms underlying regional and interannual variations in krill production in the GSL could use our WMD/surface salinity relationship with parameterize the daytime vertical distribution of *T. raschii* and *M. norvegica* populations. We quantified the amplitude of the error between a fixed depth approach and our mechanistic estimation of daytime WMD to be on par with the observed inter-regional and interspecific differences. Our study represents a first step toward a comprehensive approach for the species-specific mechanistic modelling of the response of krill to environmental forcing in the GSL.

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**References**


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Modelling the influence of daytime distribution on the transport of two sympatric krill species (*Thysanoessa raschii* and *Meganyctiphanes norvegica*) in the Gulf of St Lawrence, eastern Canada

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The Gulf of St Lawrence (GSL) provides several species of North Atlantic baleen whale with an abundant supply of krill, dominated by *Thysanoessa raschii* and *Meganyctiphanes norvegica*. We aimed to quantify the differences in upstream advection resulting from the interaction between the circulation and the specific diel vertical migration of *T. raschii* and *M. norvegica* at the scale of the northwest GSL. We coupled a regional circulation model with Lagrangian models where the daytime depth followed specific functions of surface salinity. Our results help to explain the spatio-temporal variability in both *T. raschii* and *M. norvegica* distributions. We identified in particular spatio-temporal patterns in krill upstream transport. During summer and autumn, the upstream transport of krill is steady across Jacques Cartier Strait, limited across Honguedo Strait, and more sporadic across the Estuary mouth. We estimated that the upstream advection of krill particles across the Estuary mouth would be higher by 16–17% for the *T. raschii* than for the *M. norvegica* daytime behaviour. Our results also suggest that the advective processes operating on the adults during the productive season are not the only cause for the observed magnitude of the interannual and interspecific variability in krill abundance.

**Keywords:** biophysical coupling, DVM, Gulf of St Lawrence, Krill, *Meganyctiphanes norvegica*, numerical modelling, *Thysanoessa raschii*.

**Introduction**

The Gulf of St Lawrence (GSL) is a feeding ground for several baleen whale species from the North Atlantic (Kingsley and Reeves, 1998), providing them with an abundant supply of krill, dominated by *Thysanoessa raschii* and *Meganyctiphanes norvegica*. We aimed to quantify the differences in upstream advection resulting from the interaction between the circulation and the specific diel vertical migration of *T. raschii* and *M. norvegica* at the scale of the northwest GSL. We coupled a regional circulation model with Lagrangian models where the daytime depth followed specific functions of surface salinity. Our results help to explain the spatio-temporal variability in both *T. raschii* and *M. norvegica* distributions. We identified in particular spatio-temporal patterns in krill upstream transport. During summer and autumn, the upstream transport of krill is steady across Jacques Cartier Strait, limited across Honguedo Strait, and more sporadic across the Estuary mouth. We estimated that the upstream advection of krill particles across the Estuary mouth would be higher by 16–17% for the *T. raschii* than for the *M. norvegica* daytime behaviour. Our results also suggest that the advective processes operating on the adults during the productive season are not the only cause for the observed magnitude of the interannual and interspecific variability in krill abundance.


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The Gulf of St Lawrence (GSL) provides several species of North Atlantic baleen whale with an abundant supply of forage fish, large copepods (*Calanus* spp.), and krill. Two krill species dominate the macrozooplankton biomass in the GSL: the boreal *Thysanoessa raschii* and the eurytherm *Meganyctiphanes norvegica* (Berkes, 1976). The GSL is under the influence of both Atlantic and Arctic water masses (Koutitonsky and Bugden, 1991; Saucier et al., 2003), a mix that allows for adults of both species to be found year-round in the Lower St Lawrence Estuary (LSLE) and the northern GSL (Berkes, 1976). A few regional studies in the LSLE (e.g. Simard et al., 1986b; Simard and Lavoie, 1999) and in the western GSL (Sameoto, 1976) have shown krill aggregations spread along the deep channels carved into the GSL (Figure 1a). The head of the Laurentian Channel deep inside the LSLE is one such area that hosts the aggregations of *T. raschii* and *M. norvegica* (Simard and Lavoie, 1999; Lavoie et al., 2000). Both observations (Simard et al., 1986b; Mackas et al., 1997; Santora et al., 2012) and theory of zooplankton spatial dynamics (Mackas et al., 1985; Genin, 2004) predict that krill distribution in the GSL should be dependent on topography and the spatio-temporal scales of circulation variability.

Areas of krill aggregation suitable for foraging predators in the western GSL are very dynamic (Sameoto, 1976; Lavoie et al., 2000) and difficult to predict seasonally and interannually. At a regional...
scale, the spatio-temporal pattern of krill distribution is likely to be an incidental result of the interplay between topography, prevailing currents and krill behaviour (e.g. Sourisseau et al., 2006). Both T. raschii and M. norvegica perform diel vertical migrations (DVMs) characterized by an ascent of individuals at dusk towards the food-rich surface layer and a downwards migration at dawn into the relative safety of darkness (Berkes, 1976; Simard et al., 1986a; Sourisseau et al., 2008). The DVM likely expresses a trade-off between food intake and predation risk, both higher in the surface layer (Cohen and Forward, 2009; Kaartvedt, 2010). This common zooplankton behaviour is probably the most important phenomenon of biophysical interaction in the ocean (Hays, 2003), yet our limited understanding of the mechanisms regulating DVMs in krill species hampers the study of the spatio-temporal variability in krill distribution (Murphy et al., 2004; Emsley et al., 2005; Fach and Klinck, 2006; Sourisseau et al., 2006; Cresswell et al., 2007; Lindsey and Batchelder, 2011).

The Eulerian numerical study of Sourisseau et al. (2006) followed concentrations of krill-like particles presenting different fixed swimming behaviours inside a regional circulation model of the GSL submitted to realistic atmospheric and oceanographic forcing. Their study showed how much horizontal patterns of krill distribution were dependent of the interaction between the krill vertical distribution and the sheared estuarine circulation. Krill residing within the surface layer during their DVM could not form the dense aggregations observed within the upstream LSLE but rather accumulated in the shallow southern GSL, whereas krill residing below the outflowing surface layer could. In the latter numerical experiment, krill concentrations still showed different sensitivities to the vertically sheared circulation in the LSLE–GSL system, with concentrations present within the cold intermediate layer (CIL) experiencing stronger and steadier upstream currents than those in the deep Atlantic waters below. However, this study did not consider spatio-temporal variability in the daytime weighted mean depth (WMD) of krill, nor did it discriminate the behaviour of the dominant species in the GSL.

Interspecific differences between T. raschii and M. norvegica WMD have long been observed in the GSL (Berkes, 1976). Recently, Plourde et al. (2014) identified in the LSLE–GSL system a significant relationship between both species WMD and surface salinity (Figure 1b), which controls the diffuse light attenuation through the particulate and dissolved coloured material carried by the freshwater run-off. Both species were observed deeper at higher salinity (i.e. lower diffuse attenuation), reflecting a common light-mediated control of daytime depth. In accordance with previous observations, T. raschii remained constantly higher in the water column during daytime (one-third of the observations within the CIL) than M. norvegica. However, the slopes of the relationships were significantly different between both species, so that the distance between the WMD of both species increased as salinity decreased. We hypothesize that the differences in the specific WMD interacts with the sheared circulation in the GSL (Figure 1c) to play a role in the upstream transport of krill biomass inside the LSLE. More specifically, we hypothesize that the closer association between T. raschii and the CIL favours its upstream advection compared with M. norvegica.

This paper aims to quantify at the scale of the western GSL the differences in the upstream transport resulting from the interaction between the specific daytime WMD of T. raschii and M. norvegica and the regional circulation. We coupled a regional circulation model of the GSL with two Lagrangian models for which the daytime depth of krill particles followed the specific empirical function with surface salinity from Plourde et al. (this issue). We characterized patterns of transport at the specific daytime WMD at three sections of interest in the North-West Gulf, as well as the actual fluxes of particles performing a classical DVM between their specific daytime WMD and the subsurface at night.

Material and methods
Circulation model
The ocean currents and salinity fields were obtained from the Nucleus for European Modelling of the Ocean / Ocean Parallélatin model three-dimensional hydrodynamic model of the GSL, Scotian Shelf, and Gulf of Maine (Brickman and Drozdowski, 2012). The modelling system is based on the ocean code OPA version 9.0 (Madec, 2012). The spatial resolution is 1/12’ with 46 z-levels of variable thickness in the vertical, 6 m close to the surface, and increasing with depth. It is a prognostic model, meaning that the temperature and salinity fields are free to evolve with time and are only constrained through open boundary conditions, freshwater run-off, and surface forcing. The tides are included in the model through surface elevation at the open boundaries. Freshwater enters the domain through precipitation and run-off from the 78 main rivers of the Gulf of St. Lawrence / Scotian Shelf / Gulf of Maine system including the St Lawrence River. The freshwater salinity is set to 1.0 PSU, and the freshwater temperature is set to the local ocean value causing no net heat flux due to rivers. Monthly climatologies for temperature and salinity are used to initialize the model. An annual cycle of the barotropic transport is also prescribed at Strait of Belle-Isle in addition to the baroclinic
transport calculated from the monthly temperature and salinity fields. The model has internal and external mode splitting and the time-step is 480 s for the internal mode (baroclinic) and 8 s for the external mode (barotropic). A 2005–2011 hindcast with the ocean forced by the 3-hourly Global Environmental Multiscale model from the Canadian Meteorological Centre atmospheric model output (Pellerin et al., 2003) was carried out and used to investigate circulation and transports. The windstress and surface heat fluxes are calculated at every time-step using bulk formulae based on the work of Large and Pond (1981, 1982). Model validation, circulation patterns, and transports for each season are presented in Galbraith et al. (2012) and Brickman and Drozdowski (2012).

Lagrangian model

We used daily averaged horizontal components of the currents from the NEMO-OPA regional circulation model to compute krill horizontal advection with a Runge–Kutta method, including a predictor-corrector scheme (Chasse and Miller, 2010). Daily average currents interpolated linearly in time allowed considering only the impacts of advective processes occurring at a period larger than the semi-diurnal and diurnal tidal cycles. The time-step of the Lagrangian model was 30 min because of the DVM behaviour of the particles (see below). No random walk was included on the horizontal motion. We assumed the daily average horizontal eddy diffusivity in the GSL to be similar to the Gulf of Maine, where Xue et al. (2008) demonstrated that diffusion had no major impact on lobster larval connectivity matrices at a subregional scale. We did not consider vertical advection, owing to the swimming velocities of krill being several orders of magnitude higher than vertical currents.

Diel vertical migration

We defined T. raschii and M. norvegica particles according to their daytime WMD \(Z_{\text{day}}\) (Equations (2) and (3)). Both types of particles behaved similarly for all other aspects considered in this study. We assumed that the local photoperiod modulated krill particles DVM (Tarling, 2003; Soursseaux et al., 2008). Based on the photoperiod, the proportion of a diel cycle spent close to the surface \((WMD = 15 \text{ m})\) should vary from one-third in spring to half in either spring or autumn. Individual particles’ vertical positions followed an Ornstein–Uhlenbeck process (Uhlenbeck and Ornstein, 1930). This stochastic process corresponds to a random walk modified to move back towards a mean value with the attraction increasing with distance from the mean, as can be seen in its exact numerical solution (Gillespie, 1996):

\[
Z_{t+\Delta t} = \mu + (Z_t - \mu)e^{-\Delta t} + \left(\frac{\sigma(1 - e^{-\Delta t})}{2\tau}\right)^{0.5} N(0, 1) \tag{1}
\]

where \(\mu\) was the mean value to which the process tended to revert, \(\tau\) and \(\sigma\) the mean reversion rate and volatility, \(N(0, 1)\) a normal random variable with mean 0 and variance 1, \(\Delta t\) any time-step. This algorithm allowed for a random normal distribution of the krill particles around their preferred depth, as well as for the daily adjustment required by the DVM behaviour. Here, the mean value \(\mu\) alternated between \(Z_{\text{day}}\) during daytime and 15 m during night-time, whereas the maximum speed at which particles converged towards their preferred depth \((V \approx 0.03 \text{ m s}^{-1})\) and the spread around the preferred depth \((1 \text{ s.d.} \approx 12.5 \text{ m}; \text{McQuinn, unpublished})\) were controlled by \(\tau\) \((5 \times 10^{-4} \text{ s}^{-1})\) and \(\sigma\) \((0.1 \text{ m}^2 \text{s}^{-1})\), respectively.

Specific daytime WMDs

The WMDs of T. raschii and M. norvegica adult biomass were estimated with acoustic data. Details of their acquisition and post-treatment are given in McQuinn et al. (in press, a) and Plourde et al. (2014), respectively. Daytime species-specific vertical distributions were determined in spring and summer of 2008 and 2009 in the LSLE and NWG. Conductivity, temperature, depth sampler casts near the acoustic sampling area allowed for the determination of significant relationships between the specific WMD and surface salinity (average from 0 to 10 m). In the case II waters from the LSLE–GSL system, surface salinity is an accurate index of the diffuse attenuation coefficient from non-chlorophyllous matter (Le Fouest et al., 2006; \(r^2 = 0.71\)), which always contributes more than 60% to the total diffuse attenuation coefficient (Le Fouest et al., 2010). The specific relationships between observed surface \((0–10 \text{ m})\) salinity and WMD are (Figure 1b):

\[
\begin{align*}
Z_{\text{day}} &= 11.4 \times S_{0–10\text{ m}} - 201 \quad \text{for } T. \text{ raschii} \tag{2} \\
Z_{\text{day}} &= 7.5 \times S_{0–10\text{ m}} - 64 \quad \text{for } M. \text{ norvegica} \tag{3}
\end{align*}
\]

A minimum salinity of 23 PSU was specified in the model to prevent spurious estimates of WMD in the upstream-most part of the LSLE, where freshwater run-off can be high in specific times and places. Hence, the minimum WMD was 62 m for T. raschii and 105 m for M. norvegica.

Numerical experiments

The empirical relationships between krill daytime WMD and surface salinity were based on observations limited to spring and summer. Our numerical experiments consequently spanned 1 March to 1 November. Over this period, freshwater run-off is minimum at the end of winter, then increases towards a maximum in summer (Figure 2). On the top of its marked seasonality, the GSL circulation is also characterized by a significant interannual variability (e.g., Saucier et al., 2003). Hence, we included both 2009 and 2010 in our numerical experiments as these years presented contrasting oceanographic conditions, the most striking being the record-low sea ice presence during winter 2009/2010 compared with the near average 2008/2009 winter.

We explored two types of numerical results. First, zonal velocities at the night-time depth (15 m) and at the specific daytime WMD defined by Equations (2) and (3) were extracted. Velocities allowed for a direct comparison between the potential transport of T. raschii and M. norvegica particles located at their specific WMD and for the discrimination between the relative contributions of subsurface night-time and deep daytime advection patterns on the actual transport of particles (e.g., Figure 1c). Zonal velocities at specific daytime WMD were first extracted at the scale of the whole GSL for illustrative purposes. Subsequent analyses were carried on daytime and night-time transports. “Transport” refers hereafter to the volume of water advected across three sections of interest at specific daytime and night-time depth, respectively, weighted by the seasonal photoperiod. The three sections were Jacques Cartier Strait (JCS), northern Honguedo Strait (HGS), and the northern LSLE mouth off Pointe-des-Monts (PDM; Figure 1a). Aggregations of krill typically observed the downstream of those three straits must cross these sections to eventually reach the western GSL and LSLE upstream (Sameoto, 1976; Plourde and McQuinn, 2010).

A comprehensive understanding of the krill transport in the GSL requires considering the integrated effect of daytime and
Modelling the influence of daytime distribution on the transport of two sympatric krill species

Figure 2. Simulated surface (0–10 m) salinity. (a) Spatial average over the GSL for 2009 and snapshots during (b) the maximum and (c) the minimum average salinity in 2009. Arrows in (a) situate in time snapshots in (b) and (c).

Statistics
We performed two-way ANOVAs on daytime zonal velocities across all three sections to find significant interannual, interspecific, and interaction effects. Daily zonal velocities at specific WMD were grouped at each of the three sections and for each month from March to October.

Results
Specific response to surface salinity variability
Surface salinity showed marked seasonal variability and horizontal gradient mainly forced by the spring freshet from the St Lawrence River, as illustrated by the situation in 2009 (Figure 2). Surface salinity was on average the highest at the end of winter and the lowest in midsummer (Figure 2a), and high salinities were observed year-round in the northeast GSL, while the minimum salinity was observed in the LSLE (Figure 2b and c). These results are in agreement with the monthly climatologies inferred by Petrie et al. (1996). In response to surface salinity variability, the daytime WMDs of T. raschii and M. norvegica predicted by Equations (2) and (3) were deeper and closer together in the eastern GSL in March (Figure 3a and b), and shallower and more distant in the LSLE in August (Figure 3c and d). In general, the daytime WMDs of T. raschii and M. norvegica particles were more distant in regions with lower salinities such as the LSLE and along the Gaspé buoyancy current (Figure 3a and c).

Potential transport across the western Gulf
The general surface circulation in the GSL is cyclonic. Surface circulation is enhanced by buoyancy entrainment in the first 30 m. A vertically sheared estuarine circulation is generated by freshwater run-off and enhanced by the tidal pumping at the head of the Laurentian Channel (e.g., Sauier et al., 2009, their Figure 7). The CIL is locally formed during winter and further supplied by cold waters inflowing through the Strait of Belle-Isle (Galbraith, 2006). Below, the relative isolation of the deep Atlantic layer during most spring and summer before the acceleration of the CIL erosion in autumn, results in a weak upstream residual circulation from Cabot Strait to the head of the deep Channels (Koutitonsky and Bugden, 1991; Sauier et al., 2003). The vertical shear between the surface, the intermediate, and the deep circulation regimes are particularly relevant within the framework of this study. Daytime currents for T. raschii particles were stronger in March (Figure 4a) than August (Figure 4b). However, interspecific differences in zonal daytime currents were stronger in August in the LSLE–NWG area (Figure 4b), where and when the distance between both species WMD was larger. It appeared from the pattern in advection differences that the upstream advection of T. raschii particles was enhanced in August along the north shore relative to M. norvegica particles.

Specific potential daytime transport of krill particles appeared variable in space and time. Two-way ANOVAs showed that the strongest interannual effects occurred at the PDM section (5 of 8 months), followed by the JCS (4 months) and HGS (3 months) sections (Figure 5a). The interspecific effect was significant only at PDM from late June to the end of October—the end of simulations (Figure 5b), whereas no significant interaction between years and species was detected. The absence of interspecific differences in potential daytime transport at JCS results from the bottom of the sill being shallower than the daytime depth predicted by Equations (2) and (3) (Figure 3).

Lagrangian experiments
At the PDM section in 2009, upstream fluxes of krill particles occurred during three distinct events (Figure 6). An weak inverse
linear relationship ($R^2 = 0.15$) between the average time required for the krill particles to reach the section (Figure 6a) and the number of particles that crossed the section (Figure 6b) revealed the regional dynamics of the circulation near the PDM section. Interspecific differences were the largest in June–July, with lower transit times (Figure 6a) and higher upstream fluxes for \textit{T. raschii} than \textit{M. norvegica} particles (Figure 6b). This pattern corresponded to the significant interspecific differences in potential daytime transport detected by the two-way ANOVA. However, based on daytime transport alone (Figure 6c), one would expect upstream fluxes of \textit{T. raschii} but not \textit{M. norvegica} from August to September. The discrepancies between the potential transport at daytime WMD and the particle flux resulted from the influence of night-time transport (Figure 6c). Periods without upstream particle fluxes corresponded consistently to periods of a strong night-time downstream transport at the surface. On the other hand, during the simulated period, the strongest upstream flux events occurred when both daytime and night-time transport flowed upstream together.

In 2010, the same processes operated at PDM and the broad seasonal patterns were similar to in 2009. Upstream krill particle flux was organized in discrete events that were stronger in summer, with slightly lower transit time (Figure 7a) and high fluxes of \textit{T. raschii} particles (Figure 7b). In 2010, as in 2009, potential daytime transport across PDM was stronger and mainly upstream from March to the end of July, but became weaker and more often downstream thereafter (Figure 7c). Meanwhile, the night-time transport seemed to oppose daytime’s, except for July when both coincided and generated the highest upstream flux of particles of the simulated period (Figure 7b). At shorter time-scales, however, there were differences between the 2009 and 2010 flux and transport patterns. Upstream flux events were weaker during spring 2010 than 2009, while more of them occurred throughout summer and autumn 2010 (Figure 7b), apparently driven by the night-time transport (Figure 7c).

Interspecific differences in upstream fluxes of particles were low at the HGS and JCS sections, as expected from the two-way ANOVAs on the potential daytime transport. Distinct seasonal patterns in circulation and krill particles flux appeared at both sections. The upstream flux of krill particles across HGS was limited to spring and autumn of 2009 (Figure 8b) and 2010 (not shown), during periods of upstream daytime and night-time transports (Figure 8c). During summer of both years, the circulation regime across HGS was essentially downstream and prevented the upstream advection of krill particles. On the contrary, the
upstream flux of krill particles across the JCS section started abruptly in early summer of 2009 (Figure 9b) and 2010 (not shown) and remained maximum thereafter with all the particles crossing the JCS section in less than 10 d. This pattern corresponded to a decrease in the average transit time of the particles (Figure 9a) and a significant increase in both daytime and nighttime transports across JCS during June (Figure 9c). However, the potential transport across JCS was upstream during most of the simulated period, and this suggested that during late winter and spring, mesoscale circulation processes prevented the patches to reach the JCS section a few tens of kilometres upstream.

Discussion

Daytime vertical distribution and associated transport

Our numerical results support the hypothesis that interspecific differences in daytime WMD favour the transport of T. raschi inside the LSLE. We showed that differences in specific daytime depth had significant consequences on the krill transport within the GSL, varying strongly depending on the region and season. An average surface salinity lower by two PSU at PDM relative to
HGS induced a doubling of the average daytime distance between T. raschii and M. norvegica (Table 1). This greater distance between the two species at PDM corresponded to a strong increase in the average transport at the daytime WMD of T. raschii and in the cumulated upstream flux of T. raschii particles, compared with M. norvegica (Table 1). Indeed, the greater the WMD difference between each species, the greater the potential for transport differences. But the striking daytime transport difference at PDM relative to HGS (Table 1) is also explained by a vertical shear (the rate of velocity change with depth) on average 15 times greater at the LSLE mouth than across HGS (not shown). The synergy between the estuarine residual circulation and the migration behaviour of both krill species was illustrated during most

Table 1. The average surface salinity at PDM and HGS sections in 2009 and 2010, with corresponding differences in the predicted average WMD between T. raschii and M. norvegica, the average simulated daytime transport at specific WMD, and the cumulated upstream particle flux across both sections

<table>
<thead>
<tr>
<th>Year</th>
<th>Salinity 0–10 m (PSU)</th>
<th>WMD (m)</th>
<th>Transport (10^6 m^3 d^-1)</th>
<th>Cumulative flux (particles)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PDM</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2009</td>
<td>27.6</td>
<td>-29</td>
<td>-8 (-102%)</td>
<td>2 178 (+16.2%)</td>
</tr>
<tr>
<td>2010</td>
<td>28.1</td>
<td>-27.3</td>
<td>-2 (-32.6%)</td>
<td>1 675 (+17.3%)</td>
</tr>
<tr>
<td>HGS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2009</td>
<td>30</td>
<td>-14.9</td>
<td>-1.5 (-10.3%)</td>
<td>342 (+5.1%)</td>
</tr>
<tr>
<td>2010</td>
<td>30.5</td>
<td>-13.4</td>
<td>0.1 (+0.5%)</td>
<td>385 (+3.7%)</td>
</tr>
</tbody>
</table>

Negative depth difference = shallower T. raschii WMD. Negative transport = upstream. Values in brackets are for T. raschii relative to M. norvegica.

HGS induced a doubling of the average daytime distance between T. raschii and M. norvegica (Table 1). This greater distance between the two species at PDM corresponded to a strong increase in the average transport at the daytime WMD of T. raschii and in the cumulated upstream flux of T. raschii particles, compared with M. norvegica (Table 1). Indeed, the greater the WMD difference between each species, the greater the potential for transport differences. But the striking daytime transport difference at PDM relative to HGS (Table 1) is also explained by a vertical shear (the rate of velocity change with depth) on average 15 times greater at the LSLE mouth than across HGS (not shown). The synergy between the estuarine residual circulation and the migration behaviour of both krill species was illustrated during most
of August and September 2009 when the daytime transport of T. raschii (mostly within the CIL) was upstream and M. norvegica (lower, within the Atlantic water mass) was downstream (Figure 6c). However, these opposite specific daytime transport patterns did not translate into significantly different upstream fluxes of particles, owing to the downstream subsurface night-time currents. The vertical shear was mostly negative, meaning that current velocity decreased with depth or even reversed (e.g. Figure 1c). In our results, the modelled night-time transport was on average almost three times stronger than the daytime transport at PDM.

Night-time vertical distribution and associated transport

The impact of night-time transport resulted in a two to five times lower interspecific difference in particle fluxes (16–17%) compared to the difference in daytime transport (33–102%) (Table 1). As a result, at both PDM and HGS, upstream fluxes were almost limited to periods of favourable night-time transport. Upstream fluxes were the strongest when upstream daytime and night-time transports coincided in the same direction, but night-time transport could often counteract daytime transport, especially at PDM. Our numerical results for migrating T. raschii and M. norvegica particles showed night-time transport as a key process for upstream fluxes to occur in the western GSL during the productive season. Daytime transport appeared as a modulator. Hence, the modest interspecific difference in the simulated upstream flux of krill particles within the western GSL (17% at most at PDM, Table 1) may in part result from our fixed night-time distribution and DVM timing. Krill seem generally to be located within the first 50 m of the water column at night (Kaartvedt, 2010 and references therein). Meganyctiphanes norvegica and T. raschii from the LSLE were concentrated within the first 20 m at night during a 3-day experiment in September 2003 (Sourisseau et al., 2008), coinciding with the phytoplankton distribution. It is likely that krill would target layers of high phyto- and zooplankton concentrations (Lass et al., 2001; Kaartvedt et al., 2002). In the absence of more detailed observations, our subsurface approximation for night-time WMD of krill particles (15 m) seems sensible. Clearly, ascending and descending migrations of M. norvegica, T. Raschii, and other species are generally synchronized with sunset and sunrise (Tarling, 2003; Sourisseau et al., 2008; Cohen and Forward, 2009) with some variability, and sometimes with a lag. Hence, the time spent by krill at its night-time WMD is well approximated by the seasonal photo-period, as assumed in our model.

Variability in the DVM pattern and potential effects on transport

However, sporadic alterations to the general DVM pattern have been observed in various environments and in different krill species. The life cycle (moulting, spawning) influences the proportion of the population performing DVM, the sex of individual krill influence night-time WMD, and the feeding behaviour and condition of the individuals (midnight-sinking) modify the amount of time spent by individuals at the night-time WMD (Kaartvedt, 2010, and references therein). Our results showed that short-lived alterations of night-time behaviour of M. norvegica and T. raschii could have a disproportionate impact if they resonate with transport events. An interspecific difference corresponding to a scenario of T. raschii being present within the surface layer and M. norvegica below the pycnocline at night (e.g. Bergström and Strömberg, 1997) would have important consequences, especially in the LSLE where the vertical shear is the strongest. For example, in July, when both daytime and night-time transports are mostly upstream, a 10-m difference between the night-time WMDs of M. norvegica and T. raschii could either double the interspecific difference in the upstream particle flux if T. raschii is above M. norvegica or cancel it in the opposite situation, given the vertical shear magnitude in the surface layer. Future research efforts may provide an empirical relationship between night-time WMD and a few forcing variables in the GSL, similar to the relationship of Plourde et al. (this issue) between daytime WMD and surface salinity. Comparing M. norvegica to T. raschii, we may expect a looser coupling with phytoplankton concentration owing to omnivory in M. norvegica (Berkes, 1976; Kaartvedt et al., 2002), a higher sensitivity to salinities <24 PSU (Forward and Fyhn, 1983) frequent in the LSLE’s surface layer, and a stronger negative phototaxis owing to its higher sensitivity to light (Myslinski et al., 2005). However, as our current results showed, the quantitative impact of different specific night-time WMDs on M. norvegica and T. raschii transports remains difficult to anticipate.

Regional patterns and seasonality

The information provided by our results is not readily accessible by in situ exploration. The regional patterns and seasonality in transport, the relative contributions of subsurface and deep transport, and the resulting dynamics of the krill particle flux already discussed could only be revealed through numerical modelling. During the productive part of the year (May to September; Plourde et al., 2011), the upstream advection of krill particles from the eastern to the western GSL occurred only along its north shore. HGS appeared to form a barrier to upstream advection from April to September in both 2009 and 2010. Moreover, a circulation regime shift appeared in June of both years at JCS and the mouth of the LSLE (Figure 10). Lavoe et al. (in preparation) hypothesized that this regional regime shift was driven by changes in atmospheric forcing occurring at the scale of the GSL. In our simulations, events of upstream advection across both sections were stronger and more frequent in summer and autumn than...
during late winter and spring (Supplementary material). After June, krill particles were supplied steadily to the NWG across JCS. Once there, those krill particles continued to follow the general cyclonic circulation along the north shore. Particles could eventually enter the LSLE but only according to sporadic events of upstream advection, essentially controlled by surface currents. Their alternate fate was to be entrained in the southern Gaspé current and either to be recirculated into the NWG gyre or to be flushed southeast through HGS (Figure 10). Over the simulated periods, particles whose daytime WMD followed the empirical relationship with surface salinity observed for *T. raschii* were 17% more likely to end up inside the LSLE than their *M. norvegica* counterparts.

**Interannual variability**

The comprehensive picture provided by our results must be confronted with observations. If advective processes were to dominate the distribution patterns of *M. norvegica* and *T. raschii*, the observed specific abundance variability could be interpreted as a response to the transport variability. Two datasets available to study the interspecific and interannual variability of krill in the GSL are a series of seven acoustic surveys conducted in 2008 and 2009 in the NWG and LSLE ([McQuinn et al., in press, b](#)) and the average krill egg abundance observed for ~20 years inside the LSLE ([Plourde et al., 2011](#)). According to the former set of observations, *T. raschii* was on average three times more abundant as *M. norvegica*. Assuming that the abundance of krill eggs (identified to species) reflects the abundance of krill adults ([Plourde et al., 2011](#)), *M. norvegica* and *T. raschii* were twice as abundant in 2009 than 2010. According to our simulations, the cumulated upstream flux of krill particles across PDM was 39% higher in 2009 than in 2010, whereas the interspecific difference was 17% at most. Hence, our results agree qualitatively with the observed krill biomass variability, while underestimating its amplitude.

Part of the discrepancy between the modelled and observed variability in krill abundance within the LSLE may result from the assumed night-time distribution as discussed above, but also from the absence of winter processes in our simulations. Obviously, krill advection does not stop in winter, but observations are scarce. Sea ice can considerably alter krill biomass profile, which could alter not only the WMD but the DVM behaviour itself. Hence, we decided not to extrapolate our specific daytime WMD relationship obtained during the productive season to winter, as it is likely that different forcing operates on specific vertical distributions during both periods. The omnivorous *M. norvegica* is known to seasonally target the dormant *Calanus finnarchicus* deep-dwelling stock during daytime ([Kaartvedt et al., 2002](#)), a behaviour that could contribute to interspecific differences in advection during winter. Another consequence of winter processes is that the pre-conditioning of the NWG before the general circulation shift occurring in June–July. Based on the advective regime shown at HGS (Figure 8c) and JCS (Figure 9c), we can expect krill from the eastern GSL to enter the NWG during autumn and winter. Particles could then be entrained in the NWG gyre and potentially generate considerable variation in the initial stock available for upstream advection into the LSLE the following summer. For example, [Sourisseau et al. (2006)](#) simulated in the GSL three consecutive years of the advection of krill concentrations following simplistic DVM behaviours. For their deep-dwelling scenario, i.e. no DVM (constant vertical distribution between 130 and 140 m), they found a 2-fold difference in krill abundance inside the LSLE at the end of 1998 and 1999. However, with a modified DVM behaviour (night-time ≥ 6 h), krill was not transported from the NWG into the LSLE in their model.

**Conclusion**

Our results help to explain the regional patterns in *T. raschii* and *M. norvegica* transports and to untangle the relative contributions of subsurface and deep transport to the spatio-temporal variability in krill distribution. Our results showed a regional regime shift in July that favours a subsequent upstream transport along the North Shore of the GSL during summer and autumn. During this period, the upstream transport of particles was steady across JCS, more sporadic across the Estuary mouth and limited across HGS. The night-time surface transport played an important role at the latter two sections. Our results also suggest that even if simulations agree qualitatively with observations, the observed magnitude of the interannual and interspecific variability in abundance is unlikely to be caused solely by the advective processes operating on the adults during the productive season. Simple yet important enhancements for the numerical study of biophysical interactions affecting krill distribution in the GSL would be to (i) implement a mechanistic description of night-time and winter behaviours and (ii) validate model predictions with seasonal observations of the adult segment of the population. Numerical modelling could then be used with confidence to assess the relative contribution of physical and biological/demographic processes in the transport of *M. norvegica* or *T. raschii* throughout the GSL.

**Supplementary data**

Supplementary material is available at the ICESJMS online version of the manuscript.

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Comment on “The paradox of the ‘paradox of the plankton’” by Record et al.

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The biodiversity of plankton ecosystems is no longer a paradox. The mathematical mechanisms that determine the coexistence of competitors in a general class of models, which includes almost all theoretical and applied mass conserving ecosystem models in present use, are clear. Knowledge of these mechanisms simplifies the identification and construction of models with the structural property that all species coexist for all time, irrespective of environmental forcings, spatial interactions, and further model complexities. Here, we discuss the “paradox of the ‘paradox of the plankton’” proposed by Record et al. (ICES Journal of Marine Science, 71: 236–240) and explain the mechanisms that underpin the solution.

Keywords: coexistence, competitive exclusion, linear mortality, paradox of the plankton.

Introduction

Record et al. (2013) define the “paradox of the ‘paradox of the plankton’” (Paradox II) as the dilemma facing ecosystem modellers resulting from the availability of an “abundance of viable solutions to the Paradox” but the lack of “a single mechanism [that] allows for coexistence across global, multi-trophic ocean ecosystems and across a range of spatial and temporal scales”.

Record et al. (2013) propose a solution to Paradox II in the form of a simple method to build coexistence into simple NPZ models. This approach is based on two criteria: simple form with few parameters, and the ability to reproduce observed patterns at the community level. The approach they adopted was to parameterize a generic mortality coefficient $\mu_{i}Z_{i}$, where $Z = \sum_{i}Z_{i}$, which was intended to articulate a dependence of the per capita mortality on all populations. Record et al. (2013) implemented this term in a simple zooplankton equation to demonstrate its efficacy:

$$\frac{dZ_{i}}{dt} = \gamma_{i}Z_{i} - \mu_{i}Z_{i}^{1-\phi}Z_{j}^{\phi}.$$  (1)

They then use computer simulations to show (Record et al., 2013, Figure 1) that multiple $Z$ populations coexist for long times when $0 < \phi < 1$ and suggest that the approach produces similar results when applied to phytoplankton equations and to grazing. The key argument they propose for this approach is that it allows competition to have a structuring effect on the community without excluding all but one species, and they suggest that $\phi$ provides an ability to “dial up or down the degree to which competition structures the community”.

The approach Record et al. (2013) have used certainly works to ensure the coexistence of $Z_{i}$ in their model. Here, we wish to examine why it works and why this places caveats on their claim that $\phi$ provides a mechanism to control the structure of the community. We also show that although $\phi$ is presented as encapsulating the effect of competition, this is not the mechanism that delivers coexistence in models.

The mechanisms of coexistence

The equations that describe homogeneous well-mixed populations in ecosystem models are, with few (generally unrealistic) exceptions (Huang and Zhu, 2005), of the form:

$$\frac{dx_{i}}{dt} = x_{i}f_{i}(x_{1}, x_{2}, \ldots, x_{n}).$$  (2)

This is commonly referred to as the Kolmogorov form after the early paper on the systems of this type (Kolmogorov, 1936). Here, the life function $f_{i}(x_{1}, x_{2}, \ldots, x_{n})$ describes how the $x_{i}$ population grows...
and how other populations (competitors, predators, etc.) affect its growth. Models that explicitly represent the dependence of autotroph growth on the availability of a limiting inorganic nutrient may be written in the Kolmogorov form if the mass of limiting nutrient is conserved. We note that the initial model of Record et al. [2013, Equations (1)–(3)] conserves the mass of the limiting nutrient (N) and hence may be written in the Kolmogorov form.

Cropp and Norbury (2012b) described the mathematical mechanism that ensures coexistence in ecosystem models of the Kolmogorov form. Extinction of a population \( x_i \) in models of the Kolmogorov form occurs when one or more boundary critical points \( \{x_1^*, x_2^*, \ldots, x_n^*\} \), defined by \( \sum f_j(x_1^*, x_2^*, \ldots, x_n^*) = 0 \) for all \( i \) and at which \( x_i^* = 0 \) (for some \( j \), and this is then the \( j \)th boundary), is locally stable (Kot, 2001). The local (Lyapunov) stability of a critical point is determined by the eigenvalues \( \lambda_i, i = 1, 2, \ldots, n \) of the Jacobian matrix of the system, obtained by linearizing the system equations near the critical point. Local stability requires the real parts of all the eigenvalues of the Jacobian (an \( n \times n \) equation Kolmogorov system has \( n \) eigenvalues) to be negative. One positive real part of an eigenvalue is sufficient to make a critical point unstable (Kot, 2001).

Each population \( x_i^* \) that is zero at a (boundary) critical point has an eigenvalue \( \lambda_i \in \{\lambda_1, \lambda_2, \ldots, \lambda_n\} \) associated with it for which an analytic expression is easily obtained as it is just the \( f_i \) of the population evaluated at the critical point [i.e. \( \lambda_i = f_i(x_1^*, x_2^*, \ldots, x_n^*) \), Cropp and Norbury, 2012a, b]. It is this property that reveals the mechanism that controls extinction, and consequently coexistence, in ecosystem models of the Kolmogorov form.

Coexistence of competitors is ensured if each competitor \( x_i \) has the property that its \( \lambda_i = f_i(x_1^*, x_2^*, \ldots, x_n^*) > 0 \) at every critical point where its population \( x_i^* \) is zero. This may be achieved in two ways: a parameter set may be found that ensures this property (parameterized coexistence) or the ecosystem may be composed of equations that always have the desired property over any feasible range of parameters (structural coexistence, Cropp and Norbury, 2012b).

The original postulation of the paradox of the plankton and its continuing source of interest for more than 50 years is testament to the difficulty of finding, in any given model without structural coexistence, parameter sets that deliver parameterized coexistence. Such parameter sets may not exist for some models. The classic phytoplankton competition models that embody the paradox of the plankton, such as those considered by Tilman (2007), have the property that coexistence is only possible on coincident zero isosurfaces that correspond to parameter sets for which all populations are functionally identical, the essential assumption of neutral theory (Hubbell, 2006). The probability of finding such parameter sets by randomly sampling the space of all potential parameter sets for any model is vanishingly small.

In contrast, structural coexistence is quite easy to achieve by the minor modification of parameterized models. Further, it may be done using functions commonly used to model interacting populations and (material) mass-conserving ecologies. Cropp and Norbury (2012b) classified commonly used functional forms into two types: those forms that vanish (i.e. go to zero) from a population’s \( f_i \) as the population \( x_i \) goes to zero; and those that do not. All commonly used population growth terms (including Holling types I and II) are non-vanishing and contribute positive terms to their \( f_i \). When combined with vanishing loss terms, such as Holling type III grazing and non-linear mortality, the population’s \( f_i \) will be positive at every boundary critical point. Any population described by an equation of the Kolmogorov form that has at least one non-vanishing growth term and all vanishing loss terms will never go extinct in computer simulations (Cropp and Norbury, 2012b). The simplest way to do this in cases such as Record et al. (2013) consider is via non-linear (say quadratic) mortality as a replacement for the very commonly used linear mortality.

The solution to the paradox of the plankton described by Cropp and Norbury (2012b) applies to models with any number of competing species or trophic levels, to foodwebs of any complexity, and it ensures the coexistence of competing species across all spatial and temporal scales. Further, the solution to the paradox is surprisingly simple and easy for modellers to implement in theoretical and computer models and is the general case of the solution for the particular application that Record et al. (2013) demonstrate.

**Coexistence in the Record et al. (2013) prototype**

The isolated model of Record et al. (2013) is of the Kolmogorov form as Equation (7) may be written in the form:

$$\frac{dZ_i}{dt} = Z_i f_i = Z_i (\gamma_i - \mu_i Z_i^{1-\phi} Z_i^{\phi}).$$

The mechanism that prevents \( Z_i \) from becoming extinct is the \( Z_i^{\phi} \), which causes the mortality (in this case, model closure) term to vanish as \( Z_i \to 0 \) for any value of \( \phi > 0 \). This ensures that \( \lambda_i > 0 \) at every critical point where its population \( x_i^* \) is zero. Irrespective of the veracity of any ecological arguments for \( Z_i^{1-\phi} \) (or even of its smooth modifications), it does not affect the property of long-time coexistence attributes of the population. It may be removed from the mortality term without affecting the properties that ensure coexistence, although it does modify the coexisting relative amounts of individual species. In fact, the addition of the \( Z_i^{1-\phi} \) terms for \( Z = \sum Z_j, \quad j = 1, 2, \ldots, n, \quad j \neq i \) to the \( Z_i \) equation in the absence of structural coexistence (i.e. no \( Z_i^{\phi} \) term) would make parameterized coexistence more difficult to achieve.

Record et al.’s (2013) observation that the approach they have used for mortality applies equally well to grazing should be qualified. Assuming that the prey population has a vanishing mortality term, it is the raising above one of the exponent of the prey in the numerator of the function describing the dependence of predator grazing on prey availability that is the key property that ensures the coexistence of the prey. This is independent of whether the function describes interaction or inter-dependence of the predator or prey on other populations explicitly or implicitly represented in the model.

**The role of \( \phi \) in structuring the community**

Record et al. (2013) observe that their computer simulations suggest \( \phi \) can stabilize systems and structure the community. When we analyse the mechanisms that underlie the observed numerical behaviour, we see that manipulating \( \phi \) might provide a useful “rule of thumb” for determining some community-level properties, but will not necessarily produce these properties in all models.

Increasing \( \phi \) can affect population sizes in a Kolmogorov system because each population \( x_i \) for which coexistence is guaranteed (i.e. \( \lambda_i > 0 \) whenever \( x_i^* = 0 \)) has at least one unstable eigenvector, orthogonal to the boundary, along which the population grows. The rate at which the population grows is determined by the magnitude of the \( f_i \), for Equation (3),

$$f_i = \gamma_i - \mu_i Z_i^{1-\phi} Z_i^{\phi}.$$

This becomes \( f_i = \gamma_i > 0 \), a maximum at the boundary critical point where the mortality is zero, but reduces as the system travels along the eigenvector because the growing population (in this case \( Z_i \)) causes its loss to mortality to...
increase. The mortality increases more slowly for larger values of $\phi$ and hence the population moves more rapidly away from its extinction point and maintains relatively rapid growth for longer. While the value of $\phi$ clearly affects the community structure, it is the value of $\phi$ in $Z_i^{1-\phi}$ that produces this effect. The $Z_i^{1-\phi}$, which reflects the competition between the $Z_i$, does not produce the effect but does modify it (as does the value of $\mu_i$). However, we note that the $Z_i^{1-\phi}$ reflects competition only because Record et al. (2013) have removed the explicit competition for limited resources of phytoplankton ($P$) between the $Z_i$ in their starting model [Equations (1)–(3) in their paper] and reintroduced it as implicit competition ($\overline{Z}_i^{1-\phi}$) in Equations (4)–(8).

Lyapunov stability is based on a linear approximation to a nonlinear system, and hence, the role of $\phi$ should be considered only a rule of thumb. The linear approximation is only valid "close to" critical points; as we move away from a critical point the eigenvalues and eigenvectors derived from the linear approximation lose veracity as descriptors of the system behaviour. If the system has a globally stable interior coexistence point [as Record et al.’s (2013) model appears to] then the rule of thumb is useful; however, for systems that do not have interior coexistence points, or have unstable ones, then $\phi$ only controls the minimum size to which populations fall in their "bloom-bust" cycles. Although this may also be a useful property, it could not be considered to structure the community in the way it does in the Record et al. (2013) model [see the section on pinball dynamics in Cropp and Norbury (2012b) for an extreme example of this].

We note, however, the apparent ubiquity of equilibrium solutions to models that have structural coexistence. The model simulations shown by Record et al. (2013) all have equilibrium solutions, as do the simulations shown for models with structural coexistence in Cropp and Norbury (2012b). In fact, in Cropp and Norbury (2012b), we randomly generated 4 517 053 parameter sets for NPPP, NPPZ, NPPZ, and NPZZ models with structural coexistence. Computer simulations suggest that every parameterization of every model had an equilibrium solution. We are currently not aware of a mathematical explanation for this behaviour, but it implies that the properties of the boundary critical points may be an important determinant of system dynamics in models with structural coexistence.

An alternate view on Paradox II

Record et al. (2013) propose Paradox II as the dilemma that faces NPZ modellers because of an overabundance of solutions to the paradox of the plankton. They correctly identify that, in competition models with only growth and mortality terms, the paradox of the plankton is only evident in models with exactly linear mortality terms. Competitive exclusion does not technically occur in these models for even slightly non-linear mortality, that is, in this case, for any $\phi$ that is even infinitesimally greater than zero.

As Record et al. (2013) note, there are many forms of mortality at work in populations. To our knowledge, no theoretical arguments exist that suggest that these forms are without exception exactly linear. Further, experimental measurements of per capita mortality $[(1/x_i)(dx_i/dt)]$ would have to produce results that were precisely independent of the size of the population $x_i$ to justify linearity. Any spread in the data would preclude an assumption of linearity as many regressions with non-zero slopes that were statistically indistinguishable from the zero slope case could be fitted to the data.

This apparent obsession of ecological modellers with linear mortality appears to us the real paradox of the paradox of the plankton. Linear mortality is often justified as the simplest or least biased assumption in the absence of compelling data or theory that suggests otherwise. However, exact linearity is a very precise and restrictive assumption—there is only one functional form in which mortality can be exactly linear but a potentially infinite number of forms in which it can be non-linear. Linear mortality was originally chosen for its simplicity as it typically enables explicit analytical evaluation of interior critical points.

It could be argued that the unfortunate effect of the assumption of linear mortality has been to distract ecological theory for the past 50 or so years. Hardin (1960) quotes reports of the 21 March 1944 meeting of the British Ecological Society devoted to the ecology of closely allied species that "Capt. Diver made a vigorous attack on Gause’s concept [of competitive exclusion (Gause, 1934)], on the grounds that the mathematical and experimental approaches had been dangerously over simplified.” Perhaps if Capt. Diver’s view had prevailed the paradox of the plankton would never have eventuated.

References


Plankton post-paradox: reply to comment on “The paradox of the ‘paradox of the plankton’” by Record et al.

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Classical theoretical ecology has largely focused on the coexistence of populations at the species level, particularly since the coining of the “paradox of the plankton”. The known mechanisms for coexistence, both mathematically and in nature, are myriad and diverse. Building on a dialogue in this journal (Cropp, R., and Norbury, J. 2014. Comment on “The paradox of the ‘paradox of the plankton’” by Record et al. ICES Journal of Marine Science, 71: 293–295; Record, N. R., Pershing, A. J., and Maps, F. 2014. The paradox of ‘the paradox of the plankton’. ICES Journal of Marine Science, 71: 236–240.), we outline a perspective whereby approaching the problem from a different organizational level—namely the community level—can offer valuable simplifications and insights. We expand on a prototype model that demonstrates the potential of this approach.

Keywords: biodiversity, ecosystem modelling, NPZ, paradox of the plankton, plankton.

The “paradox of the plankton” (Hutchinson, 1961, hereafter “Paradox I”) has compelled ecologists to focus on the maintenance of coexistence of competing species in ecological models. These efforts have spawned new mathematical and theoretical approaches to ecology and hence an abundance of solutions to Paradox I. Ironically, ecological modellers now face the opposite problem. Among the abundance of paradigms, there is no clear choice for how to build coexistence into models in a general way—a more pragmatic dilemma which we refer to as the “paradox of ‘the paradox of the plankton’” (Record et al., 2013, hereafter “Paradox II”). In an earlier communication (Record et al., 2013), we proposed that a solution to Paradox II should meet two criteria: (i) a simple functional form with few parameters and (ii) the ability to produce patterns observed at the community level. We constructed a prototype model—the $\phi$-model—that adds only one parameter and is able to produce community properties such as rank-abundance and abundance-distribution curves. In a follow-up communication, Cropp and Norbury (2013, hereafter “C&N”) discuss the mathematical mechanisms for coexistence in the $\phi$-model in the context of conservative Kolmogorov (CK) systems and argue more generally for the use of non-linear mortality terms to produce coexistence. Here, we provide a response, emphasizing a common ground and clarifying our broader vision.

At its core, Paradox I is a modeller’s problem. From a modeller’s point of view, much of the difficulty in coexistence has come about from the formulation of the mortality term. C&N correctly note that linear mortality is often the default assumption and that the chance of precise linearity in nature is vanishingly small. The same observations motivate our work. The original data of Gause (1932) fit more closely a non-linear curve when plotted as per capita mortality, and Lotka (1932) recognized his competitive exclusion model as a special case not in fitting with the “facts of nature”. Theoretical ecologists have thus invoked non-linear mortality terms as a solution to Paradox I (e.g. Armstrong and McGehee, 1980). Within the Kolmogoroff and CK frameworks, there is a rich literature on the coexistence of competitors (Kolmogoroff, 1936; Hirsch, 1988; Zeeman, 1993). In this sense, Paradox I is not a paradox at all, but rather a falsification of a certain subset of models for describing coexistence. If the goal is simply to build models where species coexist, then non-linear mortality in CK systems is one avenue. We have then a solution to Paradox I that predates its formulation by Hutchinson (e.g. Kostitzin, 1936).
The crux of Paradox II is not that we lack means for producing coexistence, but rather that there are many possible mechanisms. This is the case for both mathematical mechanisms, including but not limited to the type described by C&N, and true mechanisms that operate in nature. Ocean ecosystem models often have a CK core, when isolated in 0D, and the general approach of Cropp and Norbury (2012) is useful for understanding indefinite coexistence (or extinction) in this context. Ocean models also typically employ advection–diffusion–reaction equations with boundary conditions and are not of the CK form. Processes like environmental variability and advection allow species to coexist that would not coexist in a CK framework or that may coexist only as long as a certain physical feature persists (e.g. Clayton et al., 2013). Individual variability, ontogeny, and plasticity operating outside of CK frameworks provide additional mechanisms for coexistence. In fact, the chances of finding a precise CK framework in nature are also vanishingly small.

Since the penning of Paradox I, ecologists have branched out from the systems of differential equations employed by classical mathematical ecologists, describing still other mathematical mechanisms for coexistence. These include discrete system dynamics (May, 1974), stochastics (Hubbell, 2001), game theory (Doebeli et al., 2004), intraspecific demographics (Doebeli and Ispolatov, 2010), individual adaptation (Williams and Lenton, 2010), and others. It is difficult to envision a theory of biodiversity that would be complete without accounting for processes like adaptation, evolution, and speciation. Each mathematical mechanisms has the potential to elucidate true mechanisms not previously represented. This brings us to Paradox II, where we are faced with a large number of options for mathematical mechanisms for coexistence and limited knowledge of the true mechanisms of coexistence.

When it comes to ocean ecosystem models, many processes that contribute to coexistence are lumped together into a "background" mortality term. In a few cases, such as modelled predator interactions, mortality is an explicitly represented process. For the most part, however, mortality is represented heuristically. A non-linear mortality term does represent a mathematical mechanism for coexistence, as C&N point out, but it too is heuristic and does not represent a true mechanism. For those sources of mortality that are not explicitly modelled, we require a better heuristic—one that produces accurate community-level patterns but that does not overparameterize the model.

We designed our prototype model to meet these objectives. C&N have provided a thorough analysis, couching our work within their analytical framework and explaining how coexistence is maintained in the $f$-model—namely through the $Z^{+\phi}$ factor. They take exception to the $Z^{+\phi}$ factor, as it does not contribute to coexistence. Their analysis is accurate. However, coexistence is not the only objective. We also aim for a general formulation with a simple parameterization that reproduces community-level patterns. In our prototype, we designed the mortality term to produce the two limiting cases we discussed for $\phi = 0$ and $\phi = 1$—i.e. total competitive exclusion and total non-interaction. Each of the two factors captures one of these extremes, and $\phi$ provides for a continuum between the extremes.

The simple parameterization offers certain advantages. Values of $\phi$ can be determined empirically from abundance data on large communities (Figure 1) and can then be used and tested in dynamical models. We include an example for illustration where microbial communities were incubated under nutrient enriched and non-enriched conditions (details in Countway et al., 2005; Kim et al., 2011). In the non-enriched control bottles, despite rapid turnover of taxa, the rank-abundance structure of the community persisted throughout the experiment (Countway et al., 2005). The addition of nutrients produced a markedly different community structure with steeper rank-abundance curves (Kim et al., 2011). Accurately parameterizing all the ~30,000 interactions between the 238 taxa measured in these experiments represents a significant challenge and would introduce a large amount of uncertainty. By taking a community-level perspective, we may be able to reproduce these important structural differences in the community despite losing information at the taxon level.

Ultimately, we are not advocating for the particularities of a functional form, but rather for a perspective. We argue for shifting the focus, at least to some degree, away from the population level. A modeller can approach an ecosystem from multiple levels of organization, ranging from the cell (e.g. metabolic modelling) to the individual (agent-based modelling), to the population (classical equations), to the community. Each level of organization offers different insights. When choosing to model ecosystems at the population level, one assumes that the complex processes occurring at the individual level aggregate into smooth functions, and one focuses instead on how that aggregation should behave. For example, a complex and variable set of processes combine to create reproduction, which often fit approximately but not exactly to an exponential curve. Similarly, when designing terms that aggregate many population-level processes, we should focus on the community-level properties that such an aggregation should produce. We
chose the rank-abundance and abundance-distribution curves as community-level properties, and we designed our prototype therefore. Other design choices will capture other properties. In any case, they key is to approach our models from different levels of organization. Just as it is not necessary to represent every individual to capture some aspect of population dynamics, it is not necessary to represent every true mechanism for coexistence to capture some aspect of community dynamics.

Some ecologists have disparaged the enduring fixation on the idea of indefinite coexistence of species. As Hubbell (2001) wrote, “it is long past time for us to get over our myopic preoccupation with coexistence.” Hutchinson himself appeared to recognize Paradox I as a false paradox, referring to competitive exclusion as tautological and using the paradox rather as a way of framing and communicating a problem (Hutchinson, 1961). For better or worse the fixation on coexistence has underlain a rich and fruitful diversification within theoretical ecology—one that we can draw from as we move beyond coexistence, towards explaining the structure and function of communities.

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