



Emergent copepod communities in an adaptive trait-structured model



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ABSTRACT

Population dynamics for the most dominant copepod species have to some degree a mechanistic underpinning grounded in theory. However, important ecosystem shifts involve whole communities of species. Algorithms adopted from evolutionary computation provide one avenue for understanding community-level properties. We developed a pelagic copepod community model based on ecological tradeoffs in trait space, with a focus on development and growth rates, which determine fundamental properties such as size and generation length. The model is generalized to represent a broad range of possible copepod taxa. We used this framework in an adaptive-computing context to examine the different communities that assemble under different temperature and food regimes across a latitudinal gradient. Emergent communities resembled observed communities in structure and biodiversity, and showed life history strategies with clear analogs to real species.

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1. Introduction

The canonical ocean ecosystem model is the nutrient-phytoplankton-zooplankton (NPZ) model. NPZ models describe the dynamics of three state variables – nutrient, phytoplankton, and zooplankton concentrations – using a system of differential equations (Riley et al., 1949; Franks, 2002). Currently, the standard ocean ecosystem model has an NPZ model at its core, 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; Kishi et al., 2007). Because of the low number of state variables, it is feasible to embed this type of model into coupled ocean circulation models.

In the standard NPZ model, the zooplankton equation generally serves as closure, used mainly as a source of phytoplankton mortality. In this context, there is less motivation to resolve the zooplankton community more finely than a bulk abundance or biomass estimate. Yet zooplankton span seven orders of magnitude in size (10 μm to 10 m in length) and include all major phyla (~12–15 animal phyla and ~3–6 protozoan phyla) (Miller, 2004). There are complex trophic dynamics not captured by representing zooplankton using one or two functional groups, and these dynamics are particularly relevant as we move toward end-to-end

models, where the zooplankton groups influence higher trophic levels. End-to-end models have the potential to answer questions about the role of pelagic food webs in biogeochemical fluxes, and bottom-up forcing of top predators and commercially important pelagic species (Carlotti and Poggiale, 2010). A critical link in this process is the set of zooplankton state variables, which link primary production to upper trophic levels, and couple microbial scales with macro scales. Therefore it is important to investigate ways in which we might represent these groups with finer detail in models.

Among the mesozooplankton (the 0.2–20 mm constituent of zooplankton), calanoid copepods are the most numerous, are the most ubiquitous, and play a pivotal role in both the transfer of energy to higher trophic levels and the export of carbon from the euphotic layer. They have been a subject of scientific inquiry for millennia (Damkaer, 2002), and as of the turn of the last century, there were thousands of scientific articles on marine calanoid copepods (Mauchline, 1998). Thus they represent an ideal taxonomic group for more finely resolved modeling studies of community behavior.

There is a good mechanistic understanding of copepod population dynamics for the most dominant taxa. Consider, for example, the amount of work devoted to modeling the population dynamics of a single species – *Calanus finmarchicus* – in a very specific location – the Gulf of Maine (Kerfoot, 1970; Davis, 1984; Miller and Tande, 1993; Lynch et al., 1998; Miller et al., 1998; Steele and Clark, 1998; McGillicuddy et al., 2001; Zakardjian et al., 2003; Savage et al., 2004; Johnson et al., 2006; Li et al., 2006; Saumweber and Durbin, 2006; Record and Pershing, 2008; Pershing et al.,

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2009; Neuheimer et al., 2009; Record et al., 2010; Maps et al., 2012b). However, important ecological changes often take place at the community level, and involve more than just the most abundant taxa, even in *Calanus*-dominated communities (Pershing et al., 2005).

Computational models are one tool for synthesizing into a community model the many processes that govern individual species. In addition to providing numerical tools for solving complex systems of equations, more recent computational innovations provide methods for representing the adaptive and emergent properties of an ecological community. One such method is to seed models with a wide range of potentially viable organisms, described generically by sets of traits, and to model the organisms' interaction with each other and with the environment (Norberg, 2004; Follows et al., 2007). As in nature, many of the modeled organisms fail, while a small proportion succeeds, so that the diversity and structure of the community emerge from a large set of possible communities, rather than being imposed by the model design. We used this type of model to examine the different copepod communities that assemble under different temperature and food regimes in the pelagic ocean.

This adaptive trait-structured approach provides certain advantages over traditional modeling approaches. (1) It can provide insights as to where appropriate bounds should be on functional groups in simpler NPZ models; (2) it can explore a very large parameter space, where experimental information may be limited; (3) it can provide a mechanistic basis for interpolating community information on areas of the map where sampling is sparse; and (4) because of its flexibility, it may be better suited to forecast shifts in community structure in a changing climate (Follows et al., 2007). There is also potential to refine the algorithm to mimic the natural evolution of communities.

There are a number of important considerations in the design of adaptive trait-structured models. The first is the choice of traits that describe the generic organism. Traits that play important roles in ecological tradeoffs are likely to influence the structure of the community. Ecologists have used light, temperature, and nutrient requirements (Follows et al., 2007), metabolic properties (Williams and Lenton, 2007), and size (Banas, 2011). Copepods have a complex 13-stage life cycle. We used a set of traits that determine copepod development, growth, and reproduction to describe a generic copepod taxon.

A second consideration is the means of selection between modeled taxa. In this type of model, it is typical to simply select against those taxa whose population trajectories tend toward zero, or reach negligibly low levels. This approach places particular weight on the formulation of mortality. We tested combinations of five mortality terms commonly employed in copepod models. Additionally, we tested an adaptive mode, where we replaced those taxa that vanished with new, randomly generated taxa and examined the quasi-steady communities that emerged. This approach was more suitable for a large parameter space, and it allowed us to test the robustness of emergent community patterns.

This paper describes the model and examines its ability to reproduce properties of observed copepod communities. We tested the model in 0-dimensional space so that its behavior was clear and interpretable, and so that we could focus attention on exploring the trait space and modes of selection. We forced the model using temperature and food conditions both taken from the World Ocean Atlas (Conkright et al., 2002; Locarnini et al., 2010) along a latitudinal gradient from 5 to 60 ° N in the Atlantic. Validation of the model output used community-level metrics and properties. Finally, we examined the characteristics of the emergent modeled communities and compared them to observed copepod communities.

2. Methods

We began by considering a generic copepod taxon and describing its life history in terms of differential equations. We then assembled a modeled community comprised of multiple taxa, each distinguished by a unique parameterization of these equations, using parameters that quantify important life history tradeoffs. Using these modeled communities, we ran a series of computational experiments, testing the effects of the environment and of different modes of interaction on the properties of the community.

2.1. Generic copepod

We described our generic copepod using a simplified version of the “compupod” model (Maps et al., 2012a). We adopt the term “compupod” to refer to modeled or computational organisms, as opposed to real copepods. This is an important distinction, as ecologists describe trait space communities as containing analogs of real taxa, which occupy a similar region in trait space, but are not aimed at reproducing exact species (Follows et al., 2007).

At the core of pelagic copepod life history strategies are two rates: the development rate and the growth rate. The development rate (ds/dt) is the rate at which a copepod propagates through its thirteen developmental stages (s), beginning with the egg (E), passing through six naupliar stages (N1–N6), followed by six copepodid stages (C1–C6). The growth rate (dm/dt) is the rate at which a copepod accumulates mass (m). These two processes are only partially coupled in copepods, and together they determine fundamental descriptors that distinguish copepod species, such as size and generation length. Thus, an individual has two state variables – developmental stage (s), and mass (m) – both of which are functions of the environment. What follows is a derivation and explanation of the model (cf. Table 1).

2.1.1. Development rate

Copepodologists have investigated the development rate of copepods to a remarkable extent (>100 references in Mauchline, 1998). Most importantly, researchers have found and thoroughly documented a strong dependence upon temperature. At warmer temperatures, copepods progress through their developmental stages more quickly than at colder temperatures. This is true within species, and across basin-scale gradients (McLaren et al., 1969). The consequence for a population is that if temperatures increase, then the generation length will decrease. Because growth is largely uncoupled with development, a shorter generation also yields smaller animals (lower mass).

At this time, there are three main functional forms in use to describe the temperature-dependence of development rate (Record et al., 2012). We follow the formulation of Maps et al. (2012a), which derives from the temperature dependence of the Arrhenius equation (Arrhenius, 1889). The relationship, expressed in terms of development time D , is

$$D_s = d_s e^{E_D/(kT)} \quad (1)$$

where the d_s are proportionality constants for each stage, $s \in [0 = E, 1 = N1, \dots, 12 = C6]$, E_D (eV) is the cellular activation energy for development, k (eV K⁻¹) is Boltzmann's constant (Boltzmann, 1872), and T is temperature (K) (Fig. 1A). Because of the equiproportional development in copepods, for a given species, a single value of E_D applies to all stages (Mauchline, 1998). The relative stage durations, d_s , have a similar distribution for many species (Fig. 1B). There are other distributions less common among calanoids, such as isochronal, which we do not consider here. Functions of the Arrhenius form have gained widespread use in recent years with the development of the metabolic theory of ecology (Brown et al., 2004). Ecologists have used the relationship to

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