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## **COPEPOD DIAPAUSE AND THE BIOGEOGRAPHY OF THE MARINE LIPOSPHERE**

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### **ABSTRACT**

One of the primary characteristics that determines the structure and function of marine food webs is the utilization and prominence of energy-rich lipids. The biogeographic pattern of lipids throughout the ocean delineates the marine “liposphere,” which supports lipid-rich fish, mammal, and seabird communities. While the importance of lipids is well appreciated, there are no synoptic measurements or biogeographic estimates of the marine liposphere. Productive lipid-rich food webs in the pelagic ocean depend on the critical diapause stage of large pelagic copepods, which integrate lipid production from phytoplankton, concentrating it in space and time, and making it available to upper trophic levels as particularly energy-rich wax esters. As an important first step toward mapping the marine liposphere, we compared four different modeling approaches of copepodid diapause, each representing different underlying hypotheses. Through a series of global model runs, we demonstrated the potential for regional studies to be extended to estimate global biogeographic patterns of the diapause trait. In general, models were able to resolve more than just the latitudinal pattern of diapause, but also pick up a diversity of regions where diapause occurs, such as upwelling zones and seasonal seas. The predicted global biogeographic patterns, combined with carbon flux estimates, suggested a lower bound of 0.031 – 0.25 Pg C yr<sup>-1</sup> associated with copepodid diapause. While complex models may offer advantages in terms of reproducing details of community structure, simpler theoretically based models appeared to best reproduce broad-scale biogeographic patterns and showed the best correlation with observed biogeographic patterns. This indicates a promising path forward for representing a detailed biogeography of the marine liposphere in global ecosystem and climate models.

### **KEYWORDS**

diapause, copepod, trait, model, global biogeography, liposphere

## INTRODUCTION

Our understanding of the ocean ecosystem rests on a balance between complexity and simplicity (Flynn, 2005; Friedrichs et al., 2007). One approach for simplifying the biodiversity and heterogeneous information inherent to ecosystems is to organize them in terms of ecologically important characteristics, such as traits or trophic levels. For example, at a very coarse level, we often measure chlorophyll fluorescence as a way of simplifying the complex structure of a phytoplankton community. At a finer resolution, we may group organisms by traits such as size (Hansen et al., 1994), diazotrophy (Follows et al., 2007), or gelatinous body composition (Kiørboe, 2013). While simplifying in terms of these characteristics averages out some of the diversity of species, the tradeoff is that the information retained can mechanistically link the structure of the community with the ecosystem function. There have been significant steps along this path for marine phytoplankton groups using trait-based ecology (Litchman et al., 2007; Litchman and Klausmeier, 2008; Edwards et al., 2012; Barton et al., 2013). For upper trophic levels, we are still in the early stages of this process, with much of the discussion focusing on which characteristics to consider (e.g. Litchman et al., 2013). This is due partly to the complexity of life cycles and partly to the lack of a synoptic global measurement analogous to satellite measurements of phytoplankton.

One key ecosystem component that is particularly important to upper trophic levels is the utilization and prominence of energy-rich lipids. Lipids of marine origin play important ecological and biogeochemical roles in energy storage, transfer, and downward flux through processes such as the “lipid pump” (Lee et al. 2006, Jónasdóttir et al. 2015), as well as in global food security (Belton and Thilsted 2014). Yet there is little information delineating the marine liposphere—i.e. the global distribution and dynamics of these energy-rich lipids. In such a case, models have the potential to provide initial estimates. Productive lipid-rich food webs in the ocean generally depend on the critical copepodid diapause stage of large pelagic copepods, which integrate lipid production from phytoplankton, concentrating it in space and time as high energy wax esters, and making it available to upper trophic levels (Kattner & Hagen 2009). There is a wealth of information already gathered on copepodid diapause through *in situ* and modeling studies, and there is potential to produce detailed operational biogeographic maps. Here we review knowledge on copepodid diapause. Using models in the reviewed literature and a series of new global model runs, we test how existing knowledge may be extended to the basin and global scales with the intention of providing a steppingstone toward a more comprehensive trait-based perspective on the global distribution of zooplankton.

Copepods typically dominate the mesozooplankton community in most of the pelagic ocean. They form a key trophic link between primary production and upper trophic levels including fish, birds, mammals, and invertebrates. In much of the ocean, the biomass dominance of copepods takes on a particular form—that is, each community is dominated by one or a few species of large calanoid copepods whose life history is characterized by an ontogenetic vertical migration and diapause during one or several developmental stages. While most common at higher latitudes, this characterization also applies in upwelling and seasonal systems across latitudes. Copepods characterized by a late-copepodid diapause stage constitute as much as 90% of the mesozooplankton community in such ecosystems (Wishner et al., 1995; Gislason et al., 2000; Melle et al., 2014). For marine copepods, diapause is understood as an adaptation to a seasonal alternation between favorable and unfavorable conditions (Williams-Howze, 1997), conventionally viewed as an adaptation to the strong seasonality in food supply (Mauchline,

1998). However, it is likely that a combination of multiple factors, such as temperature, food supply, and predator avoidance, creates the necessary conditions for diapause (Ohman, 1988; Kaartvedt, 2000; Irigoien, 2004; Ji, 2011; Varpe, 2012).

The diapause trait is exhibited in a few different forms among marine pelagic copepods. Copepods have a 13-stage life history, including egg (E), six naupliar stages (N1-N6), and six copepodid stages (C1-C6/adult); for some species, one or more of these developmental stages may involve diapause, leading to univoltine, multivoltine, and flexible life histories, depending on diapause stage and ontogenetic rates (Fig 1). Diapause can occur in copepod eggs in sediments (also called “resting eggs”) in shallow seas (Williams-Howze, 1997) and possibly during naupliar stages (Tanimura et al., 1996). Here we focus on the lipid-rich copepodid diapause due to its essential role in the marine liposphere. Copepodid diapause is most prevalent and numerically dominant in highly seasonal systems, where primary production occurs in concentrated blooms that are limited in duration, sometimes to just a few weeks. The broader consequence of this diapause strategy is that the essential high energy resource produced by the phytoplankton bloom is concentrated in energy-rich lipids that are then available to upper trophic levels for a much longer period of time. The regions of the oceans where this strategy dominates the copepod community are also highly productive, lipid-rich food webs at higher trophic levels (Fig 2). Many of the world's most productive fisheries are derived from this lipid resource, as are the feeding habitats of migrating whales and seabirds (Varpe et al. 2005; Pershing et al. 2009; Pendleton et al. 2012; Baumgartner et al. 2013). The presence or absence of diapausing copepods plays a fundamental role on a global scale in determining whether or not a region supports a lipid-rich food web.

In many oceans, the boundary between diapause-dominated and diapause-rare communities has been shifting in strong association with climate signals and at a rate that exceeds similar climate shifts in terrestrial environments (Beaugrand et al., 2009; Chust et al., 2013). In the North Sea, the shift away from a community dominated by the diapausing copepod *Calanus finmarchicus* had a serious detrimental impact on cod recruitment, coinciding with a subsequent sharp decline of the fishery (Beaugrand, 2003). In the western North Atlantic, oceanic conditions caused a decline in *C. finmarchicus* at the southern edge of its range, with similar effects on fisheries (Pershing et al., 2005) and a decline in the calving rate of the endangered northern right whale severe enough to place the viability of the species in jeopardy (Greene and Pershing, 2004; Meyer-Gutbrod and Greene 2017). Lipid accumulation patterns through multiple higher trophic levels can have effects on condition, and therefore on foraging behavior, leading to range shifts in large pelagic species such as Atlantic bluefin tuna (Golet et al. 2015). The recent high mortality of northern right whales associated with a range shift is likely to be caused by a shift in foraging patterns (Stokstad 2017), highlighting the importance of the geographic extent of the liposphere. As ocean conditions continue to change, we might expect this lipid boundary to continue to move further into high-latitude oceans, with similar shifts in these ecosystems that depend on diapausing copepods as a critical source of energy. However, changes are likely to be more nuanced than simple latitudinal range shifts. Melting of Arctic ice can yield complex nonlinear changes, with some diapausing species relying on seasonal ice conditions and ice algae and others potentially benefitting from regions newly opened as Arctic ice retreats. Some climate models predict an increase in net primary productivity in the Arctic (Bopp et al., 2013), and the phenology of primary productivity is expected to change as well (Ji et al., 2013; Ardyna et al., 2014). There is also the possibility for one diapausing species to replace another as ranges shift. The ability to

predict where the diapause trait will persist and where it will be replaced is of primary importance in forecasting the structure of ecosystems in these regions.

There has been a great deal of research on copepodid diapause at the species level, but there are limitations to this approach that could be overcome by taking a trait-based perspective. For example, recent models of the well-studied *C. finmarchicus* rely primarily on a single study for developmental parameters (Campbell, 2001), but parameterizations and functional responses may not be consistent within this species across its range (Melle et al., 2014). Moreover, the diapause trait is flexible for this species, with diapause sometimes initiating at C5, sometimes at C4, and sometimes not at all. Another diapausing species *Calanus glacialis* exhibits similar flexibility across different Arctic regions (Daase et al., 2013). At the same time, there is evidence of hybridization between *C. finmarchicus* and *C. glacialis* (Parent et al., 2012). Species determination can be difficult or impossible in the field (Gabrielsen et al., 2012), illustrating how difficult it can be to parameterize models even for the most well-studied species. Trait-based ecology moves the focus away from species, instead asking questions like: Where and when should diapausing copepods dominate the zooplankton community? What form (i.e. during which stage, at what size, with what phenology) should this diapause strategy take in a given environment? Species of the genera *Calanus*, *Calanoides*, *Eucalanus*, *Neocalanus*, and *Rhincalanus*, among others (Table 1), play similar ecological roles, adopting diapause strategies and providing an extended and abundant lipid resource for upper trophic levels. Because the diapause trait is flexible within species, understanding the causes and geographic patterns of this trait more generically would help to understand and predict the geographic extent of the marine liposphere, and hence the distributions of productive, lipid-rich food webs. This is particularly important, as many of the regions that are undergoing the most rapid environmental change and species redistribution are also regions where diapause dominates the zooplankton community. The biogeography of the diapause trait determines the extent of the marine liposphere, and is likely to be a first-order determinant of the persistence and composition of fish, mammal, and bird communities in that region. With respect to changing climate, understanding which environments are likely to yield a copepod community that is characterized by dominance of the diapause trait, and what form the diapause strategy would take, may be more important to the resulting food web than the precise assemblage of zooplankton species.

## **METHODS**

### **Computing and mapping the marine liposphere**

The prospect of mapping trait biogeographies on basin and global scales has certain challenges. There is generally not a systematic survey with global coverage, and surveys typically enumerate species rather than traits. Barton et al. (2013) put forward three complimentary approaches to mapping trait biogeographies: (1) Directly measure the trait *in situ*; (2) Associate traits with species, and map the trait distribution back to the known distributions of species—referred to as the “trait-to-map” strategy; (3) Develop models that represent and/or predict traits in spatially-explicit environmental conditions.

For copepodid diapause, there is some potential for approach (1). The most promising methods use optical and imaging tools (Schmid et al. 2016), possibly in combination with biochemical or genetic analysis (e.g. Wagner et al., 1998). In particular, it is easy to identify deep diapause layers using *in situ* size-spectral measurements, which would enable direct measurement during

diapause. At present, only a handful of studies have attempted to map copepodid diapause across environmental gradients (Gaardsted et al., 2010; Gaardsted et al., 2011; Baumgartner et al. 2013). None of these studies covers the basin scale, but with the proliferation of autonomous profilers that include optical measurements, a global or basin scale survey of the distribution of diapausing copepods is feasible in the future. Approach (2) is sometimes used from a single-species perspective, but rarely from a trait-based perspective. Some of the most common species have range maps that can be found in the literature, particularly for the Northern Hemisphere (Fig 3, and references therein). Combining these range maps provides a coarse and static picture of the biogeography of a trait. For a higher resolution and dynamic picture, we can use approach (3). There is a large body of work modeling diapausing copepods (Hairston Jr. and Munns Jr., 1984; Huntley et al., 1994; Miller et al., 1998; Fiksen, 2000; Zakardjian et al., 2003; Tittensor et al., 2003; Speirs et al., 2006; Varpe et al., 2007; Maps et al., 2010; Maps et al., 2013; Pierson et al., 2013; Wang et al., 2014), incorporating some aspects of the trait-based perspective (Ji, 2011; Maps et al., 2012; Record et al., 2013a). Most modeling studies focus on a single region and just one species. However, the physiological controls and ecological constraints and implications of copepodid diapause should be similar across the variety of habitats where the trait is found. If this is true then the models used in regional or single-species studies should contain predictive information on the distribution of copepodid diapause more broadly.

There is a wide range of copepod models, including empirical statistical models (Reygondeau and Beaugrand, 2011; Chust et al., 2013), population dynamical and life history models (Fiksen & Carlotti 1998; McGillicuddy et al., 2001; Zakardjian et al., 2003; Speirs et al., 2006; Varpe et al., 2007; Ji et al., 2009; Record et al., 2010; Ji, 2011; Varpe, 2012), detailed individual-based models (Leising and Franks, 2000; Leising, 2001; Maps et al., 2012), and community-based models (Record et al., 2013a). In some models, life history strategies emerge, and in others, life history is assumed to be fixed. Each model is a mathematical expression of a hypothesis (or hypotheses) that attempts to explain the distribution and/or abundance in space and time of a species or to predict the combination of life history traits of a species in a given environment. The questions of where diapause will or will not occur and of how diapause boundaries will shift are global-scale questions. We would like to know if any of these models, built on basic ecological principles, can answer these questions at this scale. To this end, we have selected three contrasting copepod models that focus on diapause, each with a different underlying hypothesis, and run them on a global scale—which deliberately extends them beyond the region they were initially designed for. We have also included an empirically based model for comparison.

Each model operates in a water column context and relies on a seasonal cycle of environmental conditions. We used climatological temperature data from the World Ocean Atlas (Locarnini et al., 2010) and satellite measurements (<http://oceancolor.gsfc.nasa.gov/>) of chlorophyll to drive the model. These data are resolved to 1-degree in space and interpolated to 1 day in time. Stochastic variability was added to the seasonal cycle, and ensembles of output computed, to capture the inherent variability in conditions (following Fiksen, 2000; Ji, 2011). The models were computed essentially as they appeared in their original publications, with only minor modifications (as indicated below). It is important to note that this type of global scale test is beyond the original intent of these models as they were designed. The point of the exercise is to illustrate that the ecological principles underlying the models have broader applicability in the context of the marine liposphere. We address the modifications necessary to better generalize these models in the discussion.

## Model I: Life history

From the perspective of life history theory, the occurrence and form of a diapause strategy depends on its effect on long-term fitness (Stearns, 1992). Ji (Ji, 2011) constructed a life history model for *C. finmarchicus* diapause using lifetime offspring production per individual as a fitness measure. *C. finmarchicus* generally diapauses as a C5 copepodid, though this strategy is flexible, and during some times of year, C5s molt directly into adults for reproduction, bypassing diapause. Such a flexible strategy has confounded attempts to determine the cues for the initiation of diapause (Johnson et al., 2008). From a life history theoretical point of view, the focus in this model is not on the physiological mechanism underlying diapause, but rather on the strategy that maximizes fitness, and therefore the potential viability of the genotype or phenotype, over the long term.

### Model Description

In the Ji (Ji, 2011) model, a parameter  $p$  represents the proportion of the population entering diapause as a copepodid stage C5. The number of C5s,  $N_{C5}$ , surviving from one generation to the next is then

$$N_{C5} = p N_{C5d} + (1-p) N_{C5a}, 0 \leq p \leq 1 \quad (1)$$

where  $N_{C5d}$  is the number surviving via a diapause strategy, and  $N_{C5a}$  is the number surviving through an active (non-diapause) strategy. Net reproductive rate was calculated using a life-table approach (Kiørboe 2008). The calculation of the full life history followed the standard forms for *C. finmarchicus*. That is, an ontogenetic rate described by a Bělehrádek function (Bělehrádek, 1935) with food limitation,

$$\delta = a(T(t) + \alpha_d)^\beta / (1 - e^{(-F(t)/\phi)}) \quad (2)$$

a  $Q_{10}$  function for mortality increasing with temperature, and a food-dependent reproductive rate,

$$r(t) = \varepsilon_{\max} F(t) / (F(t) + K_F) \quad (3)$$

where  $\delta$  is development duration (days),  $r$  is reproductive rate ( $\text{day}^{-1}$ ),  $T$  and  $F$  are respectively temperature ( $^{\circ}\text{C}$ ) and food ( $\text{mg Chl-}a \text{ m}^{-3}$ ) at time  $t$ , and the other variables are parameters describing these functional shapes. One of the strengths of this model is that it requires little parameterization and yet is able to produce realistic diapause patterns. The minimal requirement for parameterization is likely to be advantageous as we attempt to project to future conditions where parameter uncertainty may be high.

## Model II: Physiology

From an individual copepod's point of view, a successful dormancy strategy requires lipid stores large enough to fulfill its metabolism during several months of starvation and to sustain the next molt, even gonad maturation and egg production in some cases. The lipid content at the onset of dormancy is often more than half of an individual's dry mass (Lee et al. 2006). Such a large amount of lipid requires individual copepods to take the diapause path well before environmental conditions become detrimental for growth. As a result, lipid metabolism is a likely candidate (even if just a proxy) for the internal control of diapause in copepods (Johnson et al., 2008). Maps (Maps et al., 2012) developed an individual-based model where individual copepods take the diapause path if they reach a minimum threshold of lipid content (tracked by carbon); otherwise, they continue development to adulthood. The variability in individual growth trajectories leads to the coexistence of both dormant and active strategies in the population. A lower lipid content threshold controls exit from diapause. Here the focus is on the physiological process controlling diapause, and it is the environmental constraints on this process that will determine whether or not diapause will occur at a location.

### Model Description

There are two aspects in the proposed control of diapause by lipid metabolism. The first is the amount of lipid stores that an individual copepod can achieve during its ontogeny. Different species have different sizes, but intraspecific variability in body size is also large. Growth and development respond differently to environmental forcing so that the cumulative difference in body size (and lipid content) can vary by as much as a factor of five seasonally and among individuals (Forster and Hirst, 2012). Maps (Maps et al., 2012) developed a generic copepod model that takes explicitly into account the growth-development tradeoff. The dynamics of the modeled copepods were determined by three core equations: Arrhenius temperature dependence, Holling type II ingestion, and allometric scaling:

$$g = 0.6I - B \quad (4)$$

$$I = F(t)v_0m(t)^{3/4}e^{-E_f/(kT(t))}/(1 + F(t)h_0v_0) \quad (5)$$

$$B = b_0m(t)^{3/4}e^{-E_b/(kT(t))} \quad (6)$$

$$\delta_s = d_s^{-1}e^{-E_d/(kT(t))}f(I) \quad (7)$$

$$f(I) = F(t)h_0v_0/(1 + F(t)h_0v_0) \quad (8)$$

$$r = gA/m_0 \quad (9)$$

with  $I$  the individual ingestion rate ( $\mu\text{g C day}^{-1}$ ),  $f(I)$  the ratio between the actual and the maximum ingestion rate that serves as a food limitation factor in the stage-specific development rate function  $\delta_s$  ( $\text{days}^{-1}$ ),  $B$  the metabolic demand ( $\mu\text{g C day}^{-1}$ ),  $g$  the growth rate ( $\mu\text{g C day}^{-1}$ ) and  $r$  the reproductive rate for an income breeding strategy (reproduction based on adult growth  $gA$ ).  $T$ ,  $F$  and  $m$  are respectively the temperature ( $^{\circ}\text{C}$ ), food ( $\mu\text{g C}$  computed from Chl- $a$ ) and body mass at time  $t$ . The other variables are parameters describing these functional shapes (note:  $k$  is Boltzmann's constant). This model was able to accurately represent ontogenetic and species-specific sizes (mass) for four calanoid copepod species (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus* and *Pseudocalanus newmani*) as a dynamic response of the model to variable temperature and food conditions. The second critical aspect of the proposed control of diapause by lipid metabolism is the rate at which the lipid stores are mobilized during dormancy (metabolic rate). A review of 15 copepod species known to rely on copepodid dormancy found that the metabolic rate of dormant copepods was about one fourth of the values for actively growing copepods, a level that remains consistent across a large range of species, body sizes, and environmental conditions (Maps et al. 2013).

### Model III: Trait-based community ecology

A copepod community is made up of many interacting species. The structure of the community emerges from complex interactions among organisms and between organisms and their environment, their prey, and their predators. In adaptive emergence models, food webs are not predefined, static structures, but rather are able to change their species composition and restructure themselves based on both changing conditions and internal dynamics. This approach has been successfully applied to phytoplankton (Follows et al., 2007; Clark et al., 2013; Daines et al., 2014) and to copepods (Record et al., 2013a). The basic approach is to describe taxa generically based on their ecologically relevant traits, and to inoculate a model environment with taxa drawn randomly or exhaustively from the corresponding parameter space. Through the dynamic processes represented in the model, selection occurs, and a small fraction of these taxa will survive and comprise the emergent community. These communities can then be compared to real communities with respect to community structure, biodiversity, and other ecological patterns. In this framework, the characteristics of diapause at a given location are a product of interactions among the full copepod community.



### Model Description

The model of Record (Record et al., 2013a) applied this approach to pelagic copepods using the following traits to describe copepod taxa: diapause stage (including non-diapause), egg mass, spawning strategy (broadcast vs. sac), baseline developmental rate, and temperature dependence of developmental rate. The model represented both stage and mass of each taxon because developmental rate (progression through stages) and growth rate (accumulation of mass) have different dependencies that are often decoupled (Maps et al. 2012). The basic equations are:

$$\delta = d_s e^{E/(kT(t))} / (1 - e^{(-F(t)/\varphi)}) \quad (10)$$

$$g = (1 - e^{-F(t)/\varphi}) \quad (11)$$

$$r = r_0(1 - e^{-F(t)/\varphi})m^{\theta_A}/m_0$$

where  $\delta$  is development time (days),  $g$  is growth rate ( $\mu\text{g C day}^{-1}$ ),  $r$  is reproductive rate,  $T$  and  $F$  are respectively temperature ( $^{\circ}\text{C}$ ) and food ( $\mu\text{g C}$  computed from Chl- $a$ ) at time  $t$ , and the other variables are parameters describing these functional shapes. In addition to these core equations, there are other relationships describing interactions between taxa, such as egg predation and cannibalism (Record et al., 2013a). Because of the coexistence and community structure reproduced in this model, it can be informative on not just the diapause strategies employed, but also the proportion of the copepod population using each strategy. The model is very computationally heavy, so a few simplifications were made to run it on a global scale. Only the diapause trait was allowed to be flexible, the number of taxa was set to 16, and the model was run out to 10 years at each pixel.

### Model IV: Empirical

A common approach to modeling the distribution of a species is to use an empirical species distribution model; we include one such example here for comparison. This approach does not attempt to represent any underlying mechanism or process, but rather uses empirical relationships between measured variables, such as temperature, and species observations. These relationships are used to map the distribution over large areas. Empirical methods have been used to estimate the distribution and range shifts of some diapausing species (Reygondeau and Beaugrand, 2011; Chust et al., 2013). There is a wide range of empirical species distribution models (e.g. generalized additive models, artificial neural networks, classification and regression trees, maximum entropy). We selected the maximum entropy model ("MaxEnt", Phillips et al., 2006), as it is designed to operate on presence-only data. We used observations from the OBIS database, which are best treated as presence-only measurements. Observations containing any species known to diapause as a copepodid were treated as presences (cf Table 1). Predictor variables included the temperature and chlorophyll- $a$  data used to force Models I-III, including the climatological temperature and chlorophyll value for each month, and the mean, median, minimum, and maximum values for the year. We used the Maximum Entropy Modeling of Species Geographic Distributions software package, version 3.3.3k (<http://www.cs.princeton.edu/~schapire/maxent/>). There are many ways to configure the MaxEnt calculation. We are showing only one such configuration here because empirical modeling is not the focus of this review; the results shown represent the best of a series of MaxEnt configurations tested. While use of MaxEnt has become widespread for mapping biogeographies of species, it has only recently been applied to map the biogeography of a trait (McGinty et al. in review).

### Data Comparison

In order to evaluate the skill of each model at producing the average biogeography of copepodid diapause, we compared the output of each to two regional copepod data sets: the North Atlantic continuous plankton recorder (CPR) dataset, and a dataset of net samples from Saito & Kubota (1995) in the Falkland Current. Datasets were chosen that spanned regions of both high and low diapause occurrence in order to give a good assessment of the model. Diapause biogeography was quantified as the proportion of large copepods (> 2 mm, Friedland et al. 2016) within the population made up of species known to have a diapause stage (cf Table 1). Model evaluation was performed by correlation of the modeled biogeography against the measured biogeography. Because the models produce different outputs that are not directly comparable, there is no completely objective way to compare them to each other. However, each produces some metric of viability of the diapause strategy. We used these metrics to compare to the prevalence of diapause in the datasets.

## RESULTS

All four models produce the very general pattern of presence of diapause at more polar latitudes and absence of diapause toward the equator (Fig 4). There are a number of regional differences. Across the North Atlantic, Model I predicts the southern boundary of the diapause range to follow the northern wall of the Gulf Stream, including a northward swing toward Iceland. Model II has a similar pattern, but also includes a band stretching from Newfoundland to the British Isles, further south than Model I. Model II also predicts gaps along the west coast of Alaska and north coast of Russia that do not appear in Model I. These two models show very similar patterns across the Southern Ocean with only subtle differences. Both predict various coastal regions to provide viable diapause habitat as well, such as the southern coasts of South America and the southwest coast of Africa along the Benguela Current. Model III is highly stochastic, and only the very general latitudinal gradient is resolved. Similarly, Model IV captures the broad latitudinal pattern, but with smoother output. Models I and II also predict a more spatially extensive biogeography of the C5 diapause trait in the northern hemisphere than in the southern, whereas model IV in particular predicted an approximate balance between the northern and southern hemispheres.

Much of the information that has gone into these models has come from our knowledge of the heavily-studied *C. finmarchicus* and other North Atlantic species. An interesting result is the fact that the models pick up on a wide range of other habitats where diapausing copepods dominate. For example, a number of diapausing species occur around the coast of South America, including *Calanus australis*, *Calanoides carinatus*, and *Calanus simillimus*, carried along the Falkland current as far north as Buenos Aires, and then diverging from the continent (Saito and Kubota, 1995). This feature is captured in Model I & II. The Yellow Sea has a summer diapause habitat for *Calanus sinicus* (Wang et al., 2003). All four models predict diapause in this region, and Model I predicts entrance into diapause to be viable as late as June. All four models also predict a stark contrast between the Black Sea (diapause habitat) and the Mediterranean Sea (not diapause habitat). This is in general agreement with reports of an abundance of *Calanus euxinus* diapausing in the Black Sea (Svetlichny et al., 2006; Unal et al., 2006), whereas the Mediterranean is characterized by a non-diapause community (Unal et al., 2006). Models I and II predict diapause in the Benguela Current, where *C. carinatus* diapauses (Arashkevich et al., 1996, Verheye et al., 2005). Models I and IV also weakly predict diapause habitat in the Arabian Sea, where *C. carinatus* diapauses (Smith, 1982). This region is characterized by an oxygen minimum zone, which likely plays a part in these ontogenetic migrations (Wishner et al., 2000); incorporating the

role of oxygen in diapause would likely improve the prediction for this region. There is generally very good correspondence between the model-predicted diapause biogeographies and the regions where the prevalence of diapause has been reported. In particular, Models I and II reproduce the detailed boundaries of the distributions of diapausing taxa. The distribution from Model III is coarser—on par with the empirical model—sacrificing spatial precision in favor of community structure.

In the northern North Atlantic and in the Falkland Current, we correlated the model output with measured distribution patterns (Fig. 5). In both cases, Model I demonstrated the strongest correlation, with notably high correlation coefficients ( $r^2 = 0.71$  and  $0.42$  respectively,  $p < 0.001$ , Table 2, Fig. 6). Models II and III had statistically significant correlations with very low  $r^2$  values in the North Atlantic, and Model IV had no significant correlation in either region (Table 2).

## DISCUSSION

The ability of these diapause models to reproduce the dominant biogeographic patterns demonstrates their potential to represent the diapause trait more generically and to predict the base of the marine liposphere on a global scale. The models tested were able to resolve more than just the latitudinal pattern of diapause, but also pick up a diversity of regions where diapause occurs, such as upwelling zones and seasonal seas. Differences in the models' performances can be traced back to different underlying assumptions and to the hypothesis implicit in each. Here we highlight two aspects: dormancy cues and mortality. There remain multiple alternative hypotheses about internal or external cues that initiate or terminate diapause across copepod species (Johnson et al., 2008; Ji, 2011), and it is possible that individuals respond to a combination of cues. The models take different approaches to parameterizing this process. For Models I and III, diapause timing is simply a function of when the diapause stage is reached; termination of diapause is based on the end of the diapause stage, calculated at a reduced development rate. Model II, in contrast, calculates termination of diapause based on body carbon as a proportion of initial body carbon. One way to resolve this discrepancy is the annual routine approach, where timing of diapause emerges as a consequence of tradeoff optimization and fitness maximization and where actors take state-dependent decisions, such as whether to and when to diapause. This approach could help yield an understanding of the mechanisms that underlie diapause phenology and how this timing relates to other activities during the rest of the year. With regard to mortality, Model I uses a temperature-dependent mortality, Model II uses temperature-dependent and allometric mortalities, and Model III uses temperature-dependent, intra-guild predation, allometric, and density dependent mortalities. These differences play a role in the different biogeographic patterns produced by the models. For example, the coarseness of the biogeographic pattern produced by Model III could be the result of using many sources of mortality, each of which is applied uniformly, but might more realistically have different degrees of importance by region. One component of future efforts in bringing these models together into a more unified perspective should be to test different assumptions of dormancy cues and mortality within different modeling frameworks. It could also be important to account for light, which determines visual predation, and influences mortality in a way that could shape large scale diapause patterns (Langbehn & Varpe 2017). These models also are all tested at a particular spatio-temporal scale to examine global biogeography. Tests at a range of finer scales, and including advection, will reveal further insights into model behavior and diapause patterns.

A better understanding of the distribution and timing of diapause has large-scale ecosystem consequences. The process of diapause affects the fate of primary production through its transfer as energy to higher trophic levels and its transfer as organic matter to the deep ocean, and may even influence primary production directly. Phytoplankton bloom initiation, termination, and/or properties may receive some level of top-down control by mesozooplankton (Behrenfeld & Boss, 2014; Friedland et al., 2016). For example, lags between phytoplankton growth and grazer responses are critical to high chlorophyll blooms in seasonal seas and upwelling regions (Behrenfeld, 2014; Behrenfeld et al., 2017). Strong predation pressure of mesozooplankton on microzooplankton may also sufficiently release phytoplankton from grazing pressure to initiate a bloom (Behrenfeld & Boss, 2014). Since emergence from diapause often occurs before the bloom peak (Johnson et al., 2008), this hypothesis is consistent with the prevalence of diapausing copepods in North Atlantic regions with strong, short phytoplankton blooms (Friedland et al., 2016). If diapausing copepods do influence phytoplankton bloom dynamics, then this relationship has important implications for phenological shifts under climate change, especially given that surface and deep conditions may change at different rates.

The phenological dimension of diapause has particular trophic importance. In seasonal environments, energy captured by primary production is often only available for a brief period. Diapause effectively acts like a battery, storing this energy and making trophic energy transfer available through a longer time period. While mesozooplankton is a better predictor of fisheries yield than net primary production (Friedland et al. 2013), a representation of transfer efficiency is required to capture differences by regions and ecosystems (Stock et al., 2017). In regions where the diapause trait is prevalent, diapausing zooplankton may account for higher transfer efficiencies through close trophic phasing (Parsons, 1988) and through their lipid content. Close trophic phasing as a tight coupling in time and/or space increases resource acquisition and leads to greater transfer of energy that would otherwise be lost as excessive production (Parsons, 1988). Moreover, the structure of the lipids themselves may improve assimilation efficiency, which would also increase transfer efficiency. Copepods at their peak lipid density provide a highly energetic food source for juvenile fishes that also need to overwinter (Heintz et al. 2013, Peterson et al. 2013). The abundance of lipid-rich versus lipid-poor zooplankton is significantly related to salmon survival in the northern California Current ecosystem (Peterson et al. 2013) and pollock survival in the eastern Bering Sea (Heintz et al. 2013). These abundances are already used (Peterson et al. 2013) or being considered as recruitment indicators in fisheries management for these populations. Hindcasts of the marine liposphere may reveal similar relationships for other populations of commercial and protected species, while forecasts would provide indices for their management. Given these considerations, the copepod diapause life history strategy may be an additional important driver of fisheries yield fluctuations that is not accounted for in present global models.

Incorporating the marine liposphere into global ecosystem models would also be important for improving carbon transfer estimates (Jónasdóttir et al. 2015). Recent carbon flux estimates for diapausing copepod species range from 2-9 gC m<sup>-2</sup> y<sup>-1</sup> for *Neocalanus tonsus* (Bradford-Grieve et al. 2001), or 3-5 gC m<sup>-2</sup> y<sup>-1</sup> for *Calanus hyperboreus* (Visser et al. 2016). Model-based estimates of the extent of the marine liposphere can help to scale these numbers up to global estimates. As a lower-bound estimate, we can use the biogeography predicted by Model I and include pixels where diapause viability is equal to one during at least one month of the year. If we assume only one diapausing species at the lowest reported flux estimate (2 gC m<sup>-2</sup> y<sup>-1</sup>), and include regions of depth greater than 1000 m, the yearly flux is 0.031 Pg C, roughly twice previous estimates

(Longhurst & Williams 1992). A more moderate estimate—using a middle value of  $5 \text{ gC m}^{-2} \text{ y}^{-1}$ , assuming two diapausing species, and lowering the diapause viability threshold to 0.5—gives a global annual flux estimate of 0.25 Pg C. Such estimates imply that diapause is an important process to include in global biogeochemical models.

Our exercise in globally extending diapause models suggests a possible role for operational modeling and climate modeling of the marine liposphere. All of these models rely primarily on input variables that are measured operationally (temperature and chlorophyll-*a*) and could potentially be modified to produce real-time or forecasted maps of the marine liposphere. The fact that the simplest (both computationally and in parameterization) of the models best reproduces biogeographic patterns is encouraging in that it might be possible to represent diapause in global ecosystem models without a prohibitive computational cost.

Ecosystem models tend to diversify over time as new hypotheses and processes are included and as new mathematical, computational, and theoretical approaches are developed. This diversification is partly due to the perspective that models should be species-centered (deYoung et al., 2004) or question-specific (Franks, 2009). Diversification of models is important because it allows us to test the boundaries of our knowledge. The danger of such diversification is that there are often many models that can produce good fits to data (Franks, 2009), and the addition of new models does not always imply improved knowledge. This dilemma is expressed in the paradox of increasing model diversity: while each new model may add knowledge, a very high diversity of models can obscure understanding of the true underlying processes (Record et al., 2013b). The converse to model diversification—convergence of models—is therefore just as important. In a strict sense, we could reject any of these models based on a failure to fit data to a desired level. A failed model, however, may still have useful elements. For example, Model III performs worse than Model I at reproducing the broad biogeography, but by bringing the community interactions from Model III into Model I or II, we could introduce richer community structure and have the ability to predict a wider range of interacting diapause strategies. We advocate for a synthesis of models rather than a selection among models. As a first step, as an outcome of an ICES working group meeting, we piloted a repository of code and commentary for zooplankton models (<http://code.google.com/p/zooplib/wiki/Introduction>). This repository has been archived, and there is a need for a collaborative forum for discussion and improvement of models, establishing a common baseline for building toward a theoretical unification of models. The next step is a collective effort by the modeling community to work out how to generalize species-focused models, to run different diapause models in different environments, to evaluate which model components are the most transportable between regions, and ultimately to synthesize the body of knowledge into a comprehensive and predictive global model of the marine liposphere. This synthesis will be key to predicting where and when productive, lipid-rich food webs will persist in future oceans.

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## CAPTIONS

Figure 1: Illustration of different diapause life history strategies, depicted over two years, including 13 developmental stages from egg to adult and showing a C5 diapause strategy, for univoltine (top), semivoltine (middle), and multivoltine/flexible (bottom) life histories. Vertical axis represents depth.

Figure 2: Northern hemisphere biogeographic patterns based on presence records in the Ocean Biogeographic Information System (OBIS) database showing diapausing copepods and lipid-rich higher trophic levels. (A) Diapausing copepod species (cf Table 1); (B) Cod species (*Arctogadus glacialis*, *Boreogadus saida*, *Gadus morhua*, *Gadus ogac*, *Gadus macrocephalus*); (C) Lipid rich forage fish (*Mallotus villosus*, *Clupea harengus*). Greyscale indicates log number of observations. The OBIS database is an aggregation of surveys, so sampling is not consistent, and the range maps shown have effort biases.

Figure 3: Northern hemisphere biogeographic patterns of copepodid diapause taken from literature estimates. (A) Diapause regions digitized from Lee et al. (Lee et al., 2006, figure 15); (B) An aggregate of species ranges from Bucklin and Lajeunesse (Bucklin and Lajeunesse, 1994) (*Calanus pacificus*, *Calanus sinicus*) and Conover (Conover, 1988) (*Calanus finmarchicus*, *Calanus glacialis*, *Calanus hyperboreus*, *Neocalanus* spp.); (C) Diapause regions digitized from Barton et al. (Barton et al., 2013, figure 5).

Figure 4: (A) Model I: The biogeography of the copepodid diapause trait under the Ji (Ji, 2011) model. Color indicates the proportion of the population, averaged over the year, entering diapause under a long-term fitness maximization assumption. (B) Model II: The biogeography of the copepodid diapause trait under the Maps et al. (Maps et al., 2012) model. Color indicates the annual mean fitness, on a log scale, of adopting a diapause strategy. (C) Model III: The biogeography of the copepodid diapause trait under the Record et al. (Record et al., 2013a) model. Color indicates the proportion of the copepod community made up of species with a late-copepodid (C4-C6) diapause. (D) The biogeography of the copepodid diapause trait under a maximum entropy model. Color indicates the habitat viability rank based on the MaxEnt algorithm.

Figure 5: Proportion of the large copepod community comprised of species that diapause for the northern North Atlantic CPR data (A), and data from Saito & Kubota (1995) (B).

Figure 6: The strongest correlation between modeled and measured diapause biogeography: Model I versus the North Atlantic CPR ( $r^2 = 0.71$ ,  $p < 0.001$ ). Shading indicates concentration of points.

Table 1: A summary of copepodid diapause strategies used by copepod species throughout the global ocean, based on multiple reviews of the topic. X = Diapause recorded; x = Dormancy recorded, but not true diapause; ? = Question mark indicated in original reference; \* = Mixture of *Calanus finmarchicus* and *Calanus helgolandicus*.

Table 2: Summary of correlation coefficients between modeled and measured diapause biogeography for the four models in the two regions. Bold text indicates  $p < 0.001$ .

	North Atlantic	Falkland Current
Model I	<b>0.71</b>	<b>0.42</b>
Model II	<b>0.04</b>	0.28
Model III	<b>0.01</b>	0.09
Model IV	0.001	0.08