SYNTHESIS

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Copepod diapause and the biogeography of the marine lipidscape

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Abstract

Aim: 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 biogeographical pattern of lipids throughout the ocean delineates the marine "lipidscape," which supports lipid-rich fish, mammal, and seabird communities. While the importance of lipids is well appreciated, there are no synoptic measurements or biogeographical estimates of the marine lipidscape. 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 towards mapping the marine lipidscape, we compared four different modelling approaches of copepodid diapause, each representing different underlying hypotheses, and evaluated them against global datasets.

Location: Global Ocean.

Taxon: Copepoda.

Methods: Through a series of global model runs and data comparisons, we demonstrated the potential for regional studies to be extended to estimate global biogeographical patterns of diapause. We compared four modelling approaches each designed from a different perspective: life history, physiology, trait-based community ecology, and empirical relationships. We compared the resulting biogeographical patterns and evaluated the model results against global measurements of copepodid diapause.

Results: Models were able to resolve more than just the latitudinal pattern of diapause (i.e. increased diapause prevalence near the poles), but to also pick up a diversity of regions where diapause occurs, such as coastal upwelling zones and seasonal seas. The life history model provided the best match to global observations. The predicted global biogeographical patterns, combined with carbon flux estimates, suggested a lower bound of 0.031–0.25 Pg C yr^{-1} of downward flux associated with copepodid diapause.

Main conclusions: Results indicated a promising path forward for representing a detailed biogeography of the marine lipidscape and its associated carbon flux in global ecosystem and climate models. While complex models may offer advantages in terms of reproducing details of community structure, simpler theoretically based

models appeared to best reproduce broad-scale biogeographical patterns and showed the best correlation with observed biogeographical patterns.

1 | 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 diverse information inherent to ecosystems is to organize around ecologically important characteristics, such as traits or trophic levels. For example, at a very coarse level, chlorophyll fluorescence is a proxy for the complex structure of a phytoplankton community. At a finer resolution, we might group organisms by size (Hansen, Bjornsen, & Hansen, 1994), diazotrophy (Follows, Dutkiewicz, Grant, & Chisholm, 2007), or body composition (Kiørboe, 2013). While simplifying can gloss over details, if done carefully, the information retained can mechanistically link community structure with ecosystem function through fitness. There have been significant steps along this path for microbes using trait-based ecology (Barton et al., 2013; Edwards, Thomas, Klausmeier, & Litchman, 2012; Litchman & Klausmeier, 2008; Litchman, Klausmeier, Schofield, & Falkowski, 2007; Record, O'Brien, Stamieszkin, & Runge, 2016). 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, Ohman, & Kiørboe, 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 particularly important to upper trophic levels is the distribution of energy-rich lipids. Marine lipids play important ecological and biogeochemical roles in energy storage, transfer, and downward flux through processes such as the "lipid pump" (Jónasdóttir, Visser, Richardson, & Heath, 2015; Lee, Hagen, & Kattner, 2006), as well as in global food security (Belton & Thilsted, 2014). Yet there is little information delineating the marine "lipidscape"—that is the global distribution and dynamics of these energy-rich lipids. Productive lipid-rich food webs in the ocean depend on the critical copepodid diapause stage of large pelagic copepods, which integrate lipid production from phytoplankton, 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 modelling studies, and there is potential to produce detailed operational biogeographical 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 towards a more comprehensive perspective on the global distribution of lipids.

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 many regions, the community is dominated by one or a few species of large calanoid copepods whose life history is characterized by diapause during one or several developmental stages. This characterization applies in high latitudes, and in upwelling and seasonal systems across latitudes. Copepods with a late-copepodid diapause stage constitute as much as 90% of the mesozooplankton community in such ecosystems (Gislason, Astthorsson, Petursdottir, Gudfinnsson, & Bodvarsdottir, 2000; Melle et al., 2014; Wishner et al., 1995). This diapause is understood as an adaptation to a seasonal alternation between favourable and unfavourable 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 factors, such as temperature, food supply, and predator avoidance, creates the necessary conditions for diapause (Irigoien, 2004; Ji, 2011; Jones & Gilbert, 2016; Kaartvedt, 2000; Ohman, 1988; Varpe, 2012).

The diapause trait is exhibited in a few different forms. 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, and the number of generations per year (ranging from many to less than one, cf Table 1) depends on diapause stage and ontogenetic rates. Diapause can occur in eggs in sediments (also called "resting eggs") in shallow seas (Williams-Howze, 1997) and possibly during naupliar stages (Tanimura, Hoshiai, & Fukuchi, 1996). Here, we focus on the lipid-rich copepodid diapause due to its essential role in the marine lipidscape. The broader consequence of this strategy is that the high-energy resource produced by brief phytoplankton blooms is concentrated in energy-rich lipids that are then available to upper trophic levels for a much longer period of time. Diapause effectively acts like a battery, storing this energy and making trophic energy transfer available through a longer time period. The regions of the oceans where this strategy dominates are also highly productive, lipid-rich food webs at higher trophic levels (Figure 1). Many of the world's most productive fisheries arise from this lipid resource, as do the feeding habitats of migrating whales and seabirds (Baumgartner et al., 2013; Heintz, Siddon, Farley, & Napp, 2013; Pendleton et al., 2012; Pershing et al., 2009; Peterson et al., 2013; Varpe, Fiksen, & Slotte, 2005). 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 lipidscape boundary has been shifting in strong association with climate signals and at a rate that exceeds similar climate shifts in terrestrial environments (Beaugrand, Luczak,

& Edwards, 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 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 & Pershing, 2004; Meyer-Gutbrod & Greene, 2017). Lipid accumulation patterns can have effects on condition, and therefore on foraging behaviour, 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 geographical extent of the lipidscape. 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 lipids 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 (Ardyna et al., 2014; Ji, Jin, & Varpe, 2013). There is also the possibility for one diapausing species to replace another as ranges shift. The ability to predict where diapause will persist, to what degree, 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, Wagner, Teegarden, Boudreau, & Durbin, 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. However, not all species exhibit the same flexibility (Table 1) and species determination can be difficult or impossible in the field because of hybridization and other factors (Gabrielsen et al., 2012; Parent, Plourde, & Turgeon, 2012), making it difficult 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 geographical patterns of this trait more generically would help to understand and predict the geographical extent of the marine lipidscape, 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 redistributions are also regions where diapause dominates the zooplankton community. The biogeography of the diapause trait determines the extent of the marine lipidscape, 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 dominantly diapausing copepod community, and what form the diapause strategy would take, may be more important to the resulting food web than the precise assemblage of zooplankton species.

1.1 | Computing and mapping the marine lipidscape

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—that is 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, Aubry, Grigor, & Fortier, 2016), possibly in combination with biochemical or genetic analysis (e.g. Wagner, Durbin, & Buckley, 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 (Baumgartner et al., 2013; Gaardsted, Tande, & Basedow, 2010; Gaardsted, Tande, & Pedersen, 2011). 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 (Figure 2, and references therein). Combining these range maps provides a rudimentary 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 modelling diapausing copepods (Fiksen, 2000; Hairston & Munns, 1984; Huntley, Zhou, & Lopez, 1994; Maps, Plourde, & Zakardjian, 2010; Maps, Record, & Pershing, 2013; Miller, Lynch, Carlotti, Gentleman, & Lewis, 1998; Pierson, Batchelder, Saumweber, Leising, & Runge, 2013; Speirs et al., 2006; Tittensor, DeYoung, & Tang, 2003; Varpe, Jørgensen, Tarling, & Fiksen, 2007; Wang, Wei,

TABLE 1 A summary of copepodid diapause strategies used by copepod species throughout the global ocean, summarizing three reviews of the topic

| Genus | Species | Stage | | | | | Gen min (years) | Gen max (years) | Reference |
		C2	C3	C4	C5	C6			
Acartia	clausi					x	0.14	0.5	Williams-Howze (1997)
Acartia	longiremis			X			0.25	0.25	Mauchline (1998)
Calanoides	acutus			X	X	X	1	1	Mauchline (1998)
Calanoides	acutus			X	X	X	1	1	Williams-Howze (1997)
Calanoides	acutus				X	X	1	1	Maps et al. (2013)
Calanoides	carinatus				X		0.14	0.33	Mauchline (1998)
Calanoides	carinatus				X		0.14	0.33	Williams-Howze (1997)
Calanoides	carinatus				X	X	0.14	0.33	Maps et al. (2013)
Calanus	australis				X				Williams-Howze (1997)
Calanus	euxinus				X	X			Maps et al. (2013)
Calanus	finmarchicus		X	X	X		0.25	1	Mauchline (1998)
Calanus	finmarchicus			X	X		0.25	1	Williams-Howze (1997)
Calanus	finmarchicus				X	X	0.25	1	Maps et al. (2013)
Calanus	glacialis		X	X	X		1	3	Mauchline (1998)
Calanus	glacialis	X	X	X	X		1	3	Williams-Howze (1997)
Calanus	glacialis			X	X	X	1	3	Maps et al. (2013)
Calanus	helgolandicus				?		0.2	0.33	Mauchline (1998)
Calanus	helgolandicus			X	X		0.2	0.33	Williams-Howze (1997)
Calanus	helgolandicus				*		0.2	0.33	Maps et al. (2013)
Calanus	hyperboreus				X		2	4	Mauchline (1998)
Calanus	hyperboreus			X	X		2	4	Williams-Howze (1997)
Calanus	hyperboreus				X	X	2	4	Maps et al. (2013)
Calanus	marshallae				X		0.25	1	Mauchline (1998)
Calanus	marshallae				X		0.25	1	Williams-Howze (1997)
Calanus	pacificus				X		0.25	0.33	Mauchline (1998)
Calanus	pacificus			X	X		0.25	0.33	Williams-Howze (1997)
Calanus	pacificus				X	X	0.25	0.33	Maps et al. (2013)
Calanus	propinquus		X	X	X	X	0.5	1	Mauchline (1998)
Calanus	propinquus			X	X		0.5	1	Williams-Howze (1997)
Calanus	propinquus				X	X	0.5	1	Maps et al. (2013)
Calanus	simillimus				X		0.5	1	Mauchline (1998)
Calanus	sinicus				X	X	0.33	1	Maps et al. (2013)
Eucalanus	bungii		X	X	X	X	1	3	Mauchline (1998)
Eucalanus	bungii				X		1	3	Williams-Howze (1997)
Eucalanus	californicus				X	X			Maps et al. (2013)
Eucalanus	monachus				X				Mauchline (1998)
Metridia	longa				x		0.5	1	Williams-Howze (1997)
Metridia	lucens				X	X	0.25	0.33	Williams-Howze (1997)
Metridia	pacifica			X	X		0.25	1	Mauchline (1998)
Neocalanus	cristatus		X	X	X		1	1	Mauchline (1998)
Neocalanus	cristatus				X		1	1	Williams-Howze (1997)
Neocalanus	cristatus				X	X	1	1	Maps et al. (2013)
Neocalanus	flemingeri			X		X	0.5	1	Mauchline (1998)
Neocalanus	flemingeri					x	0.5	1	Williams-Howze (1997)

(Continues)

TABLE 1 (Continued)

Genus	Species	Stage					Gen min (years)	Gen max (years)	Reference
		C2	C3	C4	C5	C6			
Neocalanus	*plumchrus*				X		1	1	Mauchline (1998)
Neocalanus	*plumchrus*				X		1	1	Williams-Howze (1997)
Neocalanus	*plumchrus*				X		1	1	Maps et al. (2013)
Pseudocalanus	*acuspes*		X	X	X		0.33	1	Mauchline (1998)
Pseudocalanus	*acuspes*			X	X		0.33	1	Williams-Howze (1997)
Pseudocalanus	*elongatus*		X	X	X		0.11	1	Mauchline (1998)
Pseudocalanus	*elongatus*				x		0.11	1	Williams-Howze (1997)
Pseudocalanus	*minutus*			X	X		0.5	1	Mauchline (1998)
Pseudocalanus	*minutus*				X		0.5	1	Williams-Howze (1997)
Rhincalanus	*gigas*		X	X	X	X	0.5	2	Mauchline (1998)
Rhincalanus	*gigas*					X	0.5	2	Maps et al. (2013)
Rhincalanus	*nasutus*					X	0.15	0.29	Maps et al. (2013)
Stephos	*longipes*			X	X		1	1	Mauchline (1998)

Note. X: Diapause recorded; x: Dormancy recorded, but not true diapause; ?: Question mark indicated in original reference; *: Mixture of *Calanus finmarchicus* and *Calanus helgolandicus*.
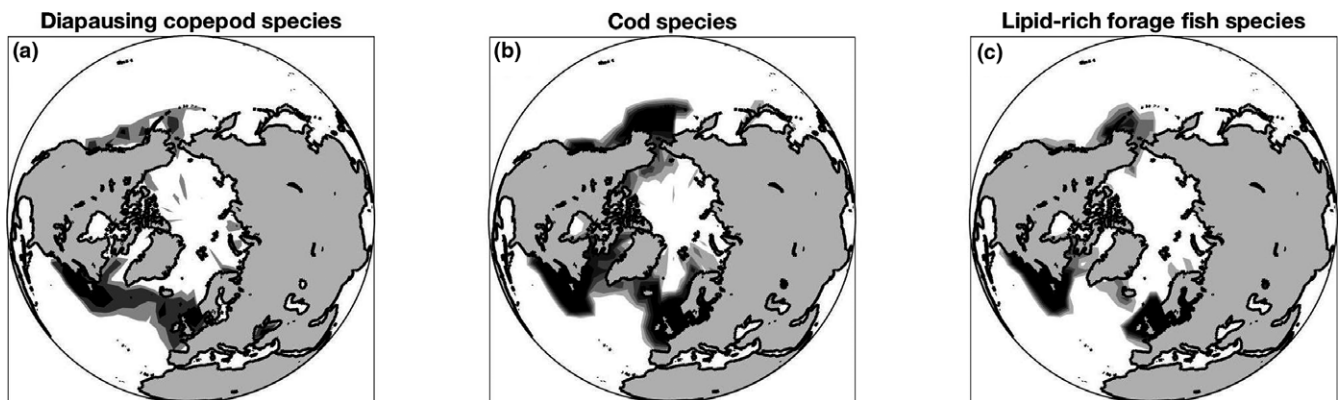

FIGURE 1 Northern hemisphere biogeographical patterns based on presence records in the Ocean Biogeographic Information System (OBIS) database showing diapausing copepods and lipid-rich higher trophic levels. (a) Diapausing copepod species (cf Table 1); (b) Cod species (*Arctogadus glacialis, Boreogadus saida, Gadus morhua, Gadus ogac, Gadus macrosephalus*); (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

& Batchelder, 2014; Wilson, Banas, Heath, & Speirs, 2016; Zakardjian et al., 2003), incorporating some aspects of the trait-based perspective (Ji, 2011; Maps, Pershing, & Record, 2012; Maps, Runge, et al., 2012; Record, Pershing, & Maps, 2013a). Most modelling 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 (Chust et al., 2013; Reygondeau & Beaugrand, 2011), population dynamical and life history models (Fiksen & Carlotti, 1998; Ji, 2011; Ji, Davis, Chen, & Beardsley, 2009; McGillicuddy et al., 2001; Record et al., 2010; Speirs et al., 2006; Varpe, 2012; Varpe et al., 2007; Zakardjian et al., 2003), detailed individual-based models (Leising, 2001; Leising & Franks, 2000; Maps, Pershing, et al., 2012; Maps, Runge, et al., 2012), and community-based models (Record, Pershing, & Maps, 2012; Record et al., 2013a). In some models, life history strategies emerge, and in others, life history is prescribed. 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.

2 | METHODS

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 regions 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 (see Supporting Information Appendix S1). 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 test whether the ecological principles underlying the models have broader applicability in the context of the marine lipidscape. We address the modifications necessary to better generalize these models in the discussion.

2.1 | 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 (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. 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.

2.2 | 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, plus gonad maturation and egg production in some cases. 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 individuals to take the diapause path well before environmental conditions
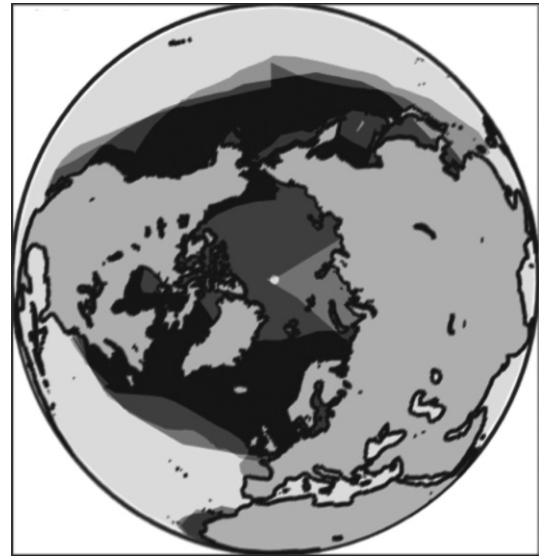

FIGURE 2 Northern hemisphere biogeographical patterns of copepodid diapause taken from literature estimates. Three overlapping ranges are shown: Diapause regions digitized from Lee et al. (2006; figure 15); An aggregate of species ranges from Bucklin and Lajeunesse (Bucklin & Lajeunesse, 1994) (*Calanus pacificus*, *Calanus sinicus*) and Conover (Conover, 1988) (*Calanus finmarchicus*, *Calanus glacialis*, *Calanus hyperboreus*, *Neocalanus* spp.); Diapause regions digitized from Barton et al. (2013, figure 5). Darkest regions indicate overlap between all three range estimates

become detrimental for growth. As a result, lipid metabolism is a likely candidate for the internal control of diapause (Johnson et al., 2008). Maps (Maps, Pershing, et al., 2012; Maps, Runge, 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 determine whether or not diapause occurs at a location. 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*). One 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 this metabolic rate 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).

2.3 | 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 (Clark, Lenton, Williams, & Daines, 2013; Daines, Clark, & Lenton, 2014; Follows et al., 2007) 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.

2.4 | Model IV: Empirical

A common approach to modelling 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 (Chust et al., 2013; Reygondeau & Beaugrand, 2011). 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, Anderson, & Schapire, 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 Modelling of Species Geographic Distributions software package, 3.3.3k. There are many ways to configure the MaxEnt calculation. We are showing only one such configuration here because empirical modelling 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, Barton, Record, Finkel, & Irwin, accepted).

2.5 | 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 and 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 modelled 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.

3 | RESULTS

All four models produce the very general pattern of presence of diapause at more polar latitudes and absence of diapause towards the equator (Figure 3). There are a number of regional differences. Across the North Atlantic, Model I (life history) predicts the southern boundary of the diapause range to follow the northern wall of the Gulf Stream, including a northward swing towards Iceland. Model II (physiology) 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 (trait-based community) is highly stochastic, and only the very general latitudinal gradient is resolved. Similarly, Model IV (empirical) 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 & Kubota, 1995). This feature is captured in Models I & II. The Yellow Sea has a summer diapause habitat for Calanus sinicus (Wang, Zuo, & Wang, 2003). All four models predict diapause in this region, and Model I predicts entrance into diapause
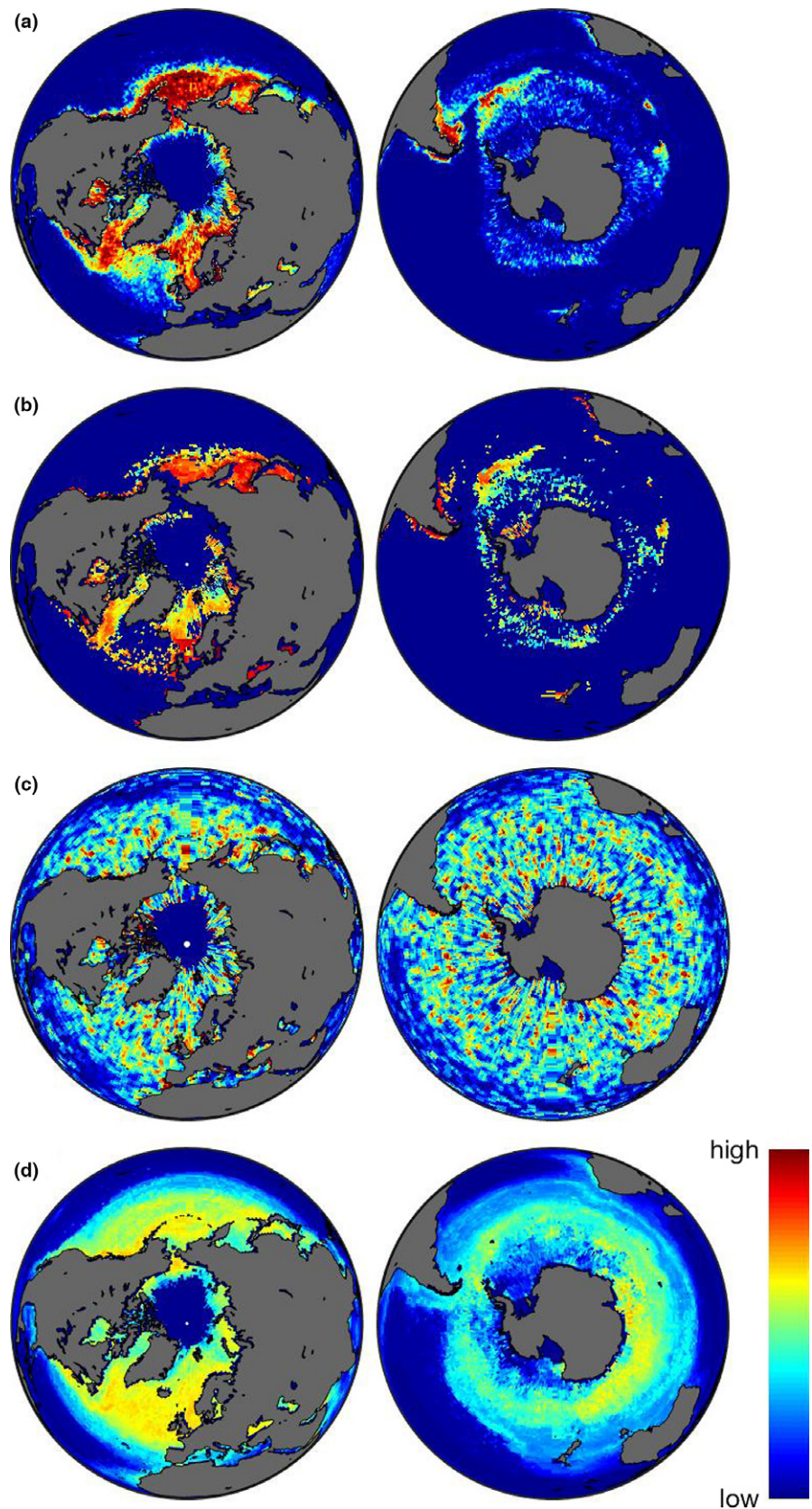
FIGURE 3 (a) Model I: The biogeography of the copepodid diapause trait under the Ji (Ji, 2011) model. Colour indicates the proportion of the population, averaged over the year, entering diapause under a long-term fitness maximization assumption. (b) Model II: The biogeography of the copepodid diapause trait under the Maps et al. (Maps, Pershing, et al., 2012; Maps, Runge, et al., 2012) model. Colour 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. (2013a) model. Colour 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. Colour indicates the habitat viability rank based on the MaxEnt algorithm [Colour figure can be viewed at wileyonlinelibrary.com]

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, Kideys, Hubareva, Besiktepe, & Isinibilir, 2006; Unal, Frost, Armbrust, & Kideys, 2006), whereas the Mediterranean is
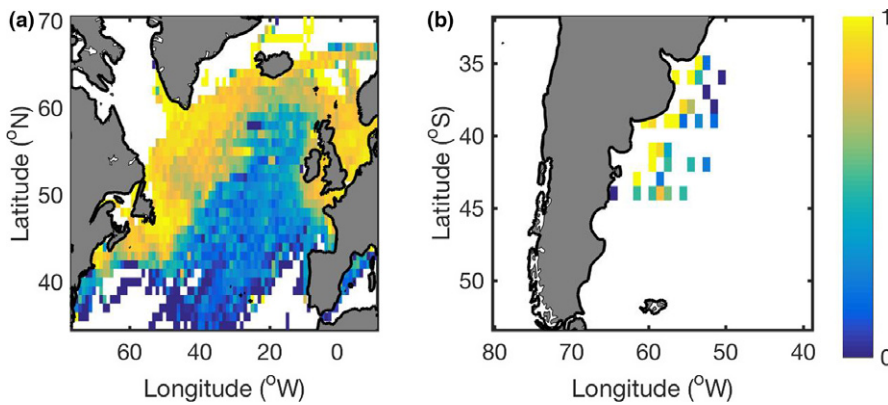
FIGURE 4 Proportion of the large copepod community comprised of species that diapause for the northern North Atlantic CPR data (a), and data from Saito and Kubota (1995) (b) [Colour figure can be viewed at wileyonlinelibrary.com]

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, Drits, & Timonin, 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, Gowing, & Gelfman, 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 favour of community structure.

In the northern North Atlantic and in the Falkland Current, we correlated the model output with measured distribution patterns (Figure 4). 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, Figure 5). 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).

4 | DISCUSSION

The ability of these diapause models to reproduce the dominant biogeographical patterns demonstrates their potential to represent the

TABLE 2 Summary of correlation coefficients (r^2) between modelled and measured diapause biogeography for the four models in the two regions. Bold text indicates $p < 0.001$

	North Atlantic	Falkland Current
Model I	**0.71**	**0.42**
Model II	**0.04**	0.28
Model III	**0.01**	0.09
Model IV	0.001	0.08

diapause trait more generically and to predict the base of the marine lipidscape 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.

One important difference between models is the formulation of dormancy timing. There remain multiple alternative hypotheses about internal or external cues that initiate or terminate diapause across copepod species (Ji, 2011; Johnson et al., 2008), 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. The strong performance of Model I suggests that a holistic approach, where diapause timing emerges from fitness-based trade-offs, might be necessary to resolve this discrepancy and to accurately model the lipidscape. If so, a major challenge will be to link this type of model with dynamical systems models that are typically used for global biogeochemistry.

A second important difference between models is the formulation of 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 biogeographical patterns produced by the models. For example, the coarseness of the biogeographical 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. While mortality studies are notoriously difficult, a key aspect of copepod diapause dynamics that requires greater effort in the future is the relative contributions of different sources of mortality, and the dependencies of those sources on changing conditions. For example, accounting for light could help our understanding of how visual predation shapes large-scale diapause patterns (Langbehn & Varpe, 2017).
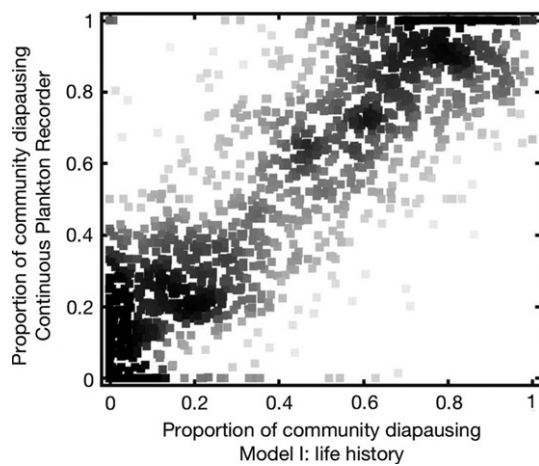
FIGURE 5 The strongest correlation between modelled and measured diapause biogeography: Model I (life history) versus the North Atlantic CPR (r^2 = 0.71, p < 0.001). Shading indicates concentration of points

Our exercise in globally extending diapause models suggests a possible role for operational modelling and climate modelling of the marine lipidscape. 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 lipidscape, which could be useful for fisheries management and conservation (Peterson et al., 2013; Stock et al., 2017). The fact that the simplest (both computationally and in parameterization) of the models best reproduces biogeographical patterns is encouraging in that it might be possible to represent diapause in global ecosystem models without a prohibitive computational cost. However, there are still challenges in understanding mortality and dormancy cues, and in linking fitness-optimization life history models with dynamical systems models. There also remains a need for local diapause studies—both in silico and in situ—particularly in the regions where these models disagree. Such studies should be placed in the context of the global perspective, and are key to refining these modelling approaches to sharpen the global picture of the marine lipidscape.

Incorporating the marine lipidscape into global ecosystem models would be important for improving carbon transfer estimates (Jónas-dóttir et al., 2015). Recent carbon flux estimates for diapausing copepod species range from 2 to 9 gC m^{-2} yr^{-1} for *Neocalanus ton-sus* (Bradford-Grieve, Nodder, Jillett, Currie, & Lassey, 2001), or 3–5 gC m^{-2} yr^{-1} for *Calanus hyperboreus* (Visser, Grønning, & Jónas-dóttir, 2016). Model-based estimates of the extent of the marine lipidscape 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 grid cells where diapause viability is equal to one during at least 1 month of the year. If we assume only one diapausing species at the lowest reported flux estimate (2 gC m^{-2} yr^{-1}), 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 gC

m^{-2} yr^{-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. It is also important to note that while copepodid diapause plays a key role in lipidscape dynamics, a complete understanding of the lipidscape will require consideration of other zooplankton species (e.g. salps, krill) as well as higher trophic levels.

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-centred (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, Pershing, & Maps, 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 towards a theoretical unification. The next step is a collective effort by the modelling 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 lipidscape. This synthesis will be key to predicting where and when productive, lipid-rich food webs will persist in future oceans.

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BIOSKETCH

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