Trophic interactions drive the emergence of diel vertical migration patterns: a game-theoretic model of copepod communities

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Abstract

Diel Vertical Migration (DVM), the daily movement of organisms through oceanic water columns, is mainly driven by spatio-temporal variations in light affecting the intensity of predator-prey interactions. Migration patterns of an organism are intrinsically linked to the distribution of its conspecifics, its prey, and its predators, each with their own fitness seeking imperatives. We present a mechanistic, trait-based model of DVM for the different components of a pelagic community. Specifically we consider size, sensory mode, and feeding mode as key traits, representing a community of copepods that prey on each other and are, in turn, preyed upon by fish. Using game theoretic principles, we explore the optimal distribution of the main groups of a planktonic pelagic food-web simultaneously. Within one single framework, our model reproduces a whole suite of observed patterns, such as size-dependent DVM patterns of copepods and reverse migrations. These patterns can only be reproduced when different trophic levels are considered at the same time. This study facilitates a quantitative understanding of the drivers of DVM, and is an important step towards mechanistically underpinned predictions of DVM patterns and biologically mediated carbon export.

Keywords— Diel Vertical Migrations, Trait-based ecology, Food-webs, Game theory, optimal strategies

Introduction

Diel Vertical Migration (DVM) is the daily movement of marine organisms between the surface and deep layers [1]. The most common pattern consists of daytime residency at depth and night-time residency in the upper part of the water column [1]. But this pattern can vary considerably, with respect to residency depths, the time spent at various depths, and the speed of ascent and descent [2, 3]. These variations occur both within and between geographical locations, and the frequent presence of two or more densely populated layers reveals the existence of multiple migrating strategies in communities [1, 4, 5].

Precisely what patterns of DVM emerge in an ecosystem depends on a variety of factors. The type of organisms involved in terms of species [4, 6], their means of detecting prey (e.g. visual or tactile) [7], life stages [3] and size

[8, 9] all influence the risk-benefit trade-off that an individual experiences at each depth during day and night, and thus its optimal DVM strategy. More subtly, the most fit strategy of an individual also depends on the abundance of the other players in the system – predators, prey and conspecifics – and the variety of strategies they undertake. With all players seeking to maximise their fitness, it is clear that all DVM strategies within an ecosystem can be interlocked giving rise to the multiple and varied patterns seen in nature.

Open ocean food-webs are usually complex, with a wide size-range of primary producers, zooplankton, and fish. A study in the California current [8] explored the DVM strategies of copepods and found that the day and night residency depths of these copepods varied systematically with their size. The smallest copepods, probably too small to be readily detected by visual predators, remain close to the surface at all times. The largest copepods, on the contrary, are likely to be conspicuous to predators even at night, and thus remain at depth all the time. In between, intermediate-sized copepods perform daily migrations of up to a hundred meters. Further, this size dependent pattern of copepod DVM varied spatially in the California Current in concert with environmental parameters such as phytoplankton biomass, stratification and water clarity. Understanding quantitatively the mechanisms behind these migrations patterns is important not only in itself, but also because DVM is a direct driver of several ecosystem functions. For example, trophic interactions within a food-web are greatly affected by migration and by the spatial and temporal overlap of predators and prey. Active carbon transport [10] is directly linked to the migration patterns of the different individuals in the water column, as they actively transport resources to the depths, providing deeper residents with valuable food resources [11] and ultimately promoting pelagic - benthic coupling. Assessing different ecosystem functions on a global scale is difficult and estimates are poorly constrained: for instance, active carbon flux in the North Atlantic ocean was found to vary between 0.3 and 7.7 $gCm^{-2}yr^{-1}$ [12, 13]. The first step to refining such estimates is to better understand the drivers of the migration patterns and of their variability.

In this work, we present a simple framework based on three fundamental traits that determine trophic interactions in the plankton, namely an organism's size, whether it is a visual or tactile predator, and its feeding mode as either an active or ambush predator. We use game theory to assess the equilibrium distribution and daily migration patterns of all groups simultaneously. Given fixed population sizes, individuals of each population can choose their position in the water column at day and at night. Their choice does not only affect their own fitness, but also the fitness of their conspecifics and of individuals from other populations. To our knowledge, this is the first time that a model recreates diel vertical migration patterns for such a wide spectrum of planktonic organisms. The model is validated by reproducing observed size-dependent patterns of copepod migrations from different locations in the California Current Ecosystem [8], and we show examples of how multiple optimal positions in the water column as well as reverse diel migration may emerge. We believe that this is also the first time that a mechanistic model is able to reproduce reverse migrations.
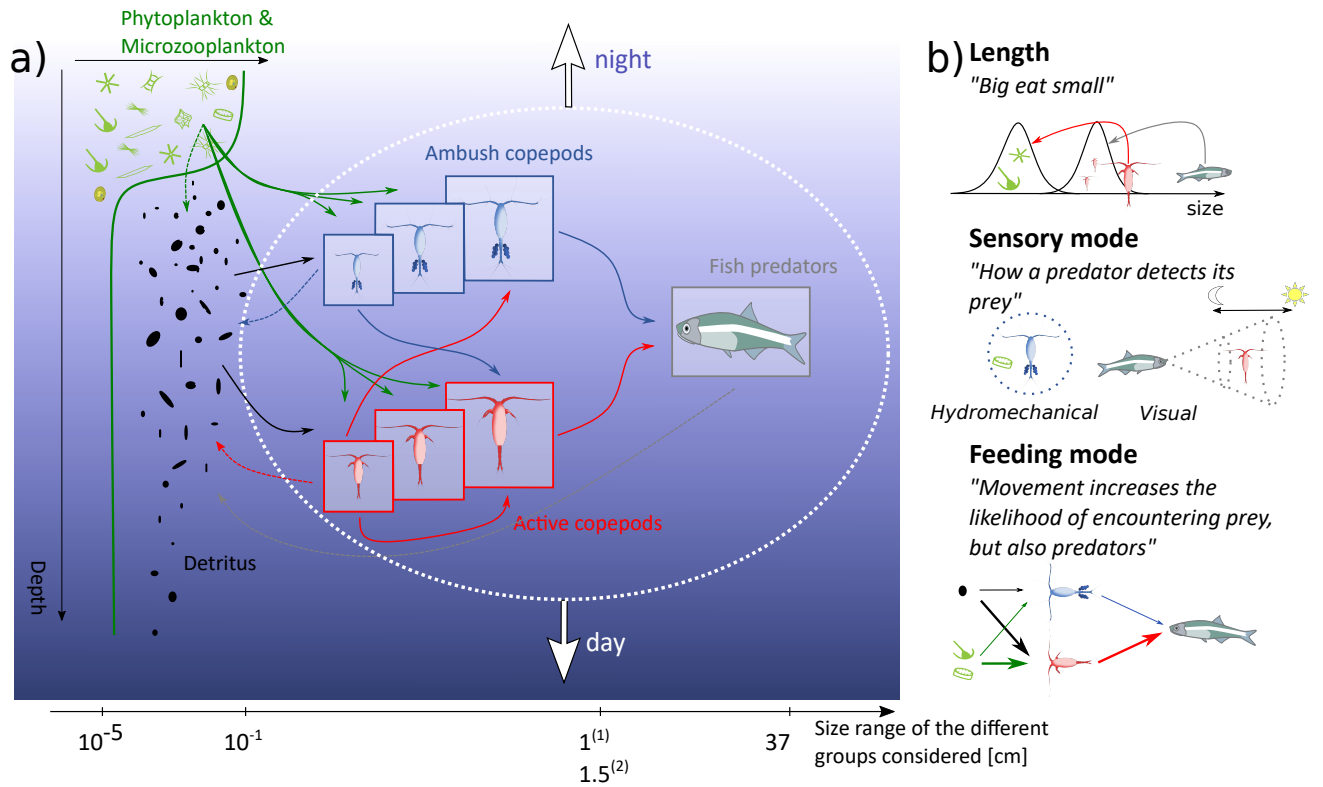
Figure 1: (a) Schematic representation of the model. We consider two classes of copepods, ambush (blue) and active (red) feeding, each sub-divided into k size classes. Copepods (tactile predators) can feed on phytoplankton, microzooplankton, detritus and smaller copepods. They are preyed upon by larger copepods and fish (visual predators). Note that the arrows indicate interactions but not their intensities, which are dictated by many factors (e.g., environmental conditions such as light levels, abundances of the different groups in the layer considered, size-preference functions). In order to maximise their fitness, all copepods and fish can adjust their vertical position individually at day and at night (example arrows here are for normal migration patterns, but reverse migrations and residency are also possible strategies). [1] in the body-length axis is for environmental scenarios 1-5, and [2] for environmental scenario 6. (b) The main influences of the three key traits (length, sensory mode, feeding mode) on predator-prey interactions.

Methods

Community set-up

The model considers a simple pelagic food-web consisting of phytoplankton, microzooplankton, copepods, and fish. We include particulate detritus created by the various components of this food web. The copepod community is divided into two feeding modes (ambush and active feeding), each further divided into a number of size classes (figure 1 (a)). Copepods can feed on phytoplankton and microzooplankton that are abundant near the surface, on smaller copepods (depending on size and feeding mode), and on the rain of particulate detritus produced by the overlaying community. In turn, copepods are predated by larger copepods (again, size and feeding mode rules apply) and visually feeding fish. Throughout the water column, copepods experience different conditions (concentration of phytoplankton, microzooplankton and detritus, light levels) that impact both their access to food and exposure to predators. Light conditions vary between day and night, and copepods and fish are all allowed to undertake DVM, each seeking their optimal strategy balancing feeding opportunity against risk. Since population dynamics are not considered, we make the simplification that the size distribution of organisms follows a Sheldon spectrum (i.e. equal biomass in groups of equal logarithmic size ranges [14]). We note that the general approach is not dependent on this assumption, although it does reduce our parameter space in that fixing the phytoplankton biomass in the water column also fixes the biomass of all other groups. We also make the simplifying assumption that active feeding copepods constitute about 65% of the smallest size classes (total length 1mm) but almost 100% of the largest (total length 1cm), consistent with observations reported in a copepod database [15] (see S.I. 1 for more details).

The vertical distribution of phytoplankton (and microzooplankton) is prescribed with a typical profile - high in the surface and depleted at depths [16], while all other organisms in the model can adjust their position in the water column freely at day and at night. The goal of an organism's DVM strategy is to maximise its fitness, which is defined as a trade-off between growth and mortality [17, 18]. Growth and mortality terms are derived from feeding interactions between all individuals (figure 1 (a)) that are described mechanistically with simple assumptions (prey size spectra, visual or tactile predation defining the clearance rates of organisms), see figure 1 (b) for a schematic representation of how traits influence these interactions and S.I. 1 for a complete mathematical description of these interactions. Growth is equal to the assimilation rate (the ingestion rate modulated by an assimilation efficiency) minus a metabolic cost and a migration cost. Mortality is due to direct predation and to a background mortality term (i.e. predation from higher non-modelled trophic levels). Active copepods have a high encounter rate with prey as they sweep out a greater search volume per unit time than passive copepods that have to rely solely on the movement of their prey to bring about encounters (figure 1 (a)). Active feeding, however, has a downside in that it also increases the encounter rate with predators as well as incurring a higher metabolic cost [19]. Preference functions of active and passive copepods are also different, active copepods generally eating relatively bigger prey than passive copepods [20]. Moreover, all organisms create detrital particulate material, which sinks and can be taken up again by flux feeding copepods [21]. All things being equal, the encounter of flux feeding copepods with detrital material increases with depth due to coagulation that increases particle size and sinking speed [22]. A comprehensive description of the different rates, interactions and parameters is provided in

98 S.I. 1.

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Optimal migration patterns

101 For each group of migrating organisms (i.e., within the same size range and feeding mode; each "organism box" of
102 figure 1 (a)), we want to know the proportion that follows each possible strategy ij (that is, being in water layer
103 i during daytime and j during night-time). To this end, each group λ is allocated a strategy matrix $\mathbf{n}^\lambda = n_{ij}^\lambda$,
104 where n_{ij}^λ is the proportion of organisms from the group λ following strategy ij. The optimal distribution is
105 the set of matrices $\mathbf{n}^{\lambda*}$ that simultaneously maximise the fitness of all groups, with the additional property that
106 within each group, the fitness for each occupied strategy (i.e. $\mathbf{n}^{\lambda*} > 0$) is identical and greater than the fitness
107 for each unoccupied strategy (i.e. $\mathbf{n}^{\lambda*} = 0$). The optimal distribution of one group is obviously dependent on the
108 distribution of all other groups, and the equilibrium of all groups is termed the Nash equilibrium [23]. This equi-
109 librium is the point where no individual from any group can change its strategy without decreasing its own fitness.

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111 The Nash equilibrium is derived using the replicator equation [16, 24]. In short, the replicator equation allows
112 each subgroup of individuals following a particular strategy to grow proportionally to its corresponding fitness.
113 At each iteration, the biomass of all groups is renormalized to ensure that no biomass is added to the system.
114 The algorithm is iterated many times (approx. $2 \cdot 10^6$), until it has converged. Because of the complexity of
115 our model, the system reached an attractor but not a perfectly stable equilibrium in the presented simulations:
116 some groups exhibited oscillations around an average distribution (see S.I. 1 and figure S2 for more details). As a
117 consequence, the results we present are averages of the distributions when the system has converged. Sensitivity
118 analyses were performed on the most uncertain parameters (light saturation parameter for fish visual range, slope
119 of the size spectrum, depth-dependent detritus preference function, size-dependent proportion of ambush and
120 active copepods) of the model to test its robustness (S.I. 1).

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Definition of environmental scenarios

123 As a test case, we use size-dependent migration patterns observed in the California Current Ecosystem [8]. We
124 created 5 environmental scenarios (ES) corresponding to the environmental conditions encountered at 5 different
125 oceanic locations, ordered from clear, oligotrophic conditions to more eutrophic, turbid ones. These environmental
126 scenarios corresponded to the oceanic conditions encountered by Ohman and Romagnan at the time and locations
127 of their study [8]. They assessed these patterns with a fine depth and size resolution, providing an ideal test of
128 the robustness of our model to different oceanic conditions (figure 2 (a)). Between the different scenarios, only a
129 few environmental parameters varied: the surface phytoplankton concentration, the depth of the mixed layer z_0,
130 the extent of the transition zone z_m from nutrient-rich to nutrient poor waters, the total biomass of the system,
131 the light attenuation coefficient, and the surface detritus concentration (table 1). These environmental parame-
132 ters match the measured oceanic conditions reported when the migration patterns were observed [8, 25]. A 6th
133 environmental scenario was created, reflecting conditions observed in a temperate fjord, Dabob Bay (Washington,

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USA). This environmental scenario is particularly interesting as reverse migration of small copepods was observed in this fjord [26, 27]. Tactile predators up to 1.5cm long have been reported there, and we increased our size-range of zooplankton for that scenario so that our model matches the observed distribution.

Table 1: Glossary of parameters used for the 6 Environmental Scenarios (ES)

Parameter	Unit	Signification	ES 1	ES 2	ES 3	ES 4	ES 5	ES 6
P_0	$gC \ m^{-3}$	Phytoplankton surface concentration	0.042	0.16	0.27	0.65	0.74	0.23
z_0	m	Mixed layer depth	100	100	60	50	50	30
z_m	m	Sharpness of the transition zone	60	60	30	10	10	10
k_{light}	m^{-1}	Attenuation coefficient	0.03	0.07	0.1	0.2	0.6	0.1
SD	$gC \ m^{-3}$	Surface detritus concentration	0.005	0.02	0.03	0.06	0.1	0.05

Results

The general trends of the DVM patterns of copepods observed in the California Current (figure 2(a), [8]) are reproduced by our model (figure 2(b)) under similar environmental conditions (table 1). The smallest copepods remain close to the surface (between 0 and 20m) without performing DVM. Their residency in this layer is more or less constant across environmental scenarios. The biggest copepods do not migrate either, remaining at depth day and night. Their residency varies from more than 400m for the open ocean to less than 100m for the most nearshore, turbid location. In between, intermediate-sized copepods (total length between approximately 2 and 7mm) undertake DVM. The day and night positions of these copepods get closer to the surface as the conditions get more eutrophic (i.e. more turbid), and the amplitude of migration also decreases: the biggest migration amplitude decreases from almost 100m (offshore-like conditions) to about 10m. With regards to feeding mode, it is active copepods that primarily undertake DVM, while passive feeders remain close to the surface at day and at night (figure 3).

Fish on the contrary display different behaviours depending on the conditions, but with very little or no clear DVM patterns. For very clear waters (ES 1), they display no major difference in their distribution between day and night: they are most numerous close to the surface, and their abundance steadily decreases until 300m, where their concentration suddenly becomes very low. In the 2nd ES, fish do not exhibit strong DVM either, with day and night distributions confined to the upper 120 m with a weak maximum at around 80–100m deep. ES 3 displays a peak concentration around 30m, and decreases up to 100m, beyond which the concentration is almost null. The distribution of fish in ES 4 shows a peak at the surface before a strong decline, but with day-night differences: the day distribution is bimodal, with a second (lower) maximum around 80m. At night, fish that are part of this second peak migrate up between 0 and 50m. In the last environmental scenario, fish mainly remain close to the surface, and a few remain day and night at depths up to 50m.

For the environmental scenario 6, three migration regimes are observed: no migration patterns and resi-
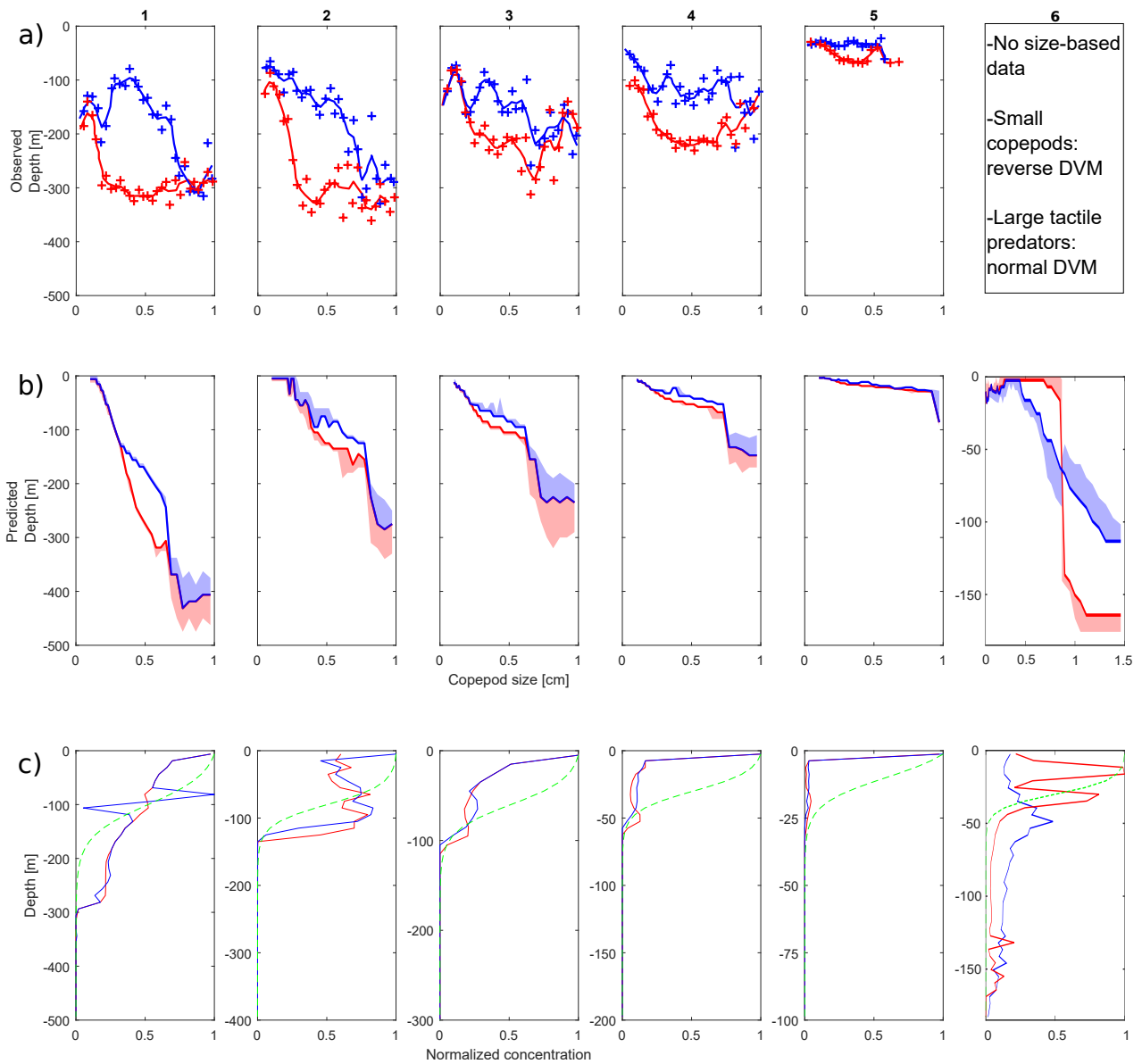
Figure 2: a) Weighted mean depth as a function of copepod body size by day (red) and night (blue) at five different locations in the California Current. Points indicate means of duplicate profiles, and lines loess fits. Migration patterns are arranged from offshore clear water (left) to onshore more turbid waters (right). Data redrawn from Ohman and Romagnan 2016 [8]. b) Simulated size-dependent median (and 1st and 3rd quartile—shaded areas) position of copepods at day (red) and night (blue) for conditions similar to the ones of the 5 experimental migration patterns of panel a. c) Simulated day (red) and night (blue) normalized fish distribution as well as prescribed normalized abundance of phytoplankton and microzooplankton (dashed green) in the water column. Note the change in vertical axis scale in the different figures of panel c.
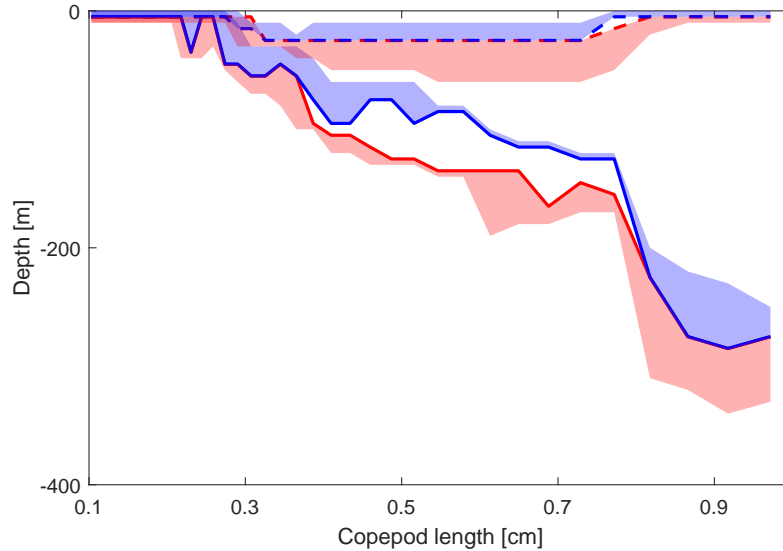
Figure 3: Modelled day (red) and night (blue) distribution of active and passive copepods in ES 2. Active copepods exhibit DVM (solid lines), while passive copepods remain at the surface (dashed lines).

dency close to the surface for the smallest organisms (between 0.1 and 0.4cm), reverse migration patterns for intermediate-sized organisms (between 0.4 and 0.8cm), and normal DVM patterns for the biggest ones (0.8 to 1.5cm). Note that no residency at depth was found here for the biggest organisms.

Discussion

Our model successfully recreates the migration trends observed for different size classes of interacting copepods across a gradient of environmental conditions [8, 26]. The few discrepancies between observed and modelled patterns can be due to simplifications in our setup or uncertainties in the model parametrisation. For example, our vertical structure of phytoplankton and microzooplankton distribution near the surface is highly idealised. In particular, it is relatively common that the maximum phytoplankton abundance (and indeed maximum primary production) is sub-surface [28, 29]. The maximum depth available to fish (and probably to large copepods) could also be limited by an Oxygen Minimum Zone [4]. Further, we opted for a simple myopic fitness measure [30] and we do not consider ontogeny; but different life stages have different fitness goals, and their fitness measure varies accordingly. Despite these simplifications, our model captures the DVM behaviours of a full community only driven by environmental conditions and trophic interactions.

Trophic interactions as a DVM driver

To our knowledge, only two previous mechanistic models investigated DVM for more than one trophic level with a fine depth resolution, and both considered zooplankton prey interacting with planktivorous fish [16, 31]. Pinti and Visser [16], in agreement with our study, found that zooplankton have three main migration regimes: surface residency under low predation pressure, DVM under intermediate predation pressure and residency at depth

under high predation pressure. However, when the food-web becomes more complex (e.g. figure 2), it can be difficult to judge which organisms will have the highest predation pressure, and, thus, which migration regimes will emerge. Nevertheless, it is clear that organisms can only remain at depth if there is food available there. In our case, sinking detritus provided the largest copepods with the resources they need to survive at depth without migrating (cf. sensitivity analysis in the supplementary material). DVM patterns of fish are also very different from those reported in this previous study and in many field studies (see e.g. [6, 32]): fish generally exhibit a much more pronounced DVM than our results show. This may be because DVM of forage fish is not only driven by prey abundance but also by their predators. While zooplankton in our model are effectively subject to frequency-dependent mortality (i.e. a dense layer of prey attracts more predators), fish are not subject to the same process, being exposed only to a constant mortality risk representing top predators. The absence of these potentially migrating top predators in our simulations may explain why only few fish undertake DVM. Planktivorous fish DVM is here only triggered by a bottom-up approach, and adding explicitly top predators may induce a stronger DVM response due to an added top-down control.

There have been only a few observational studies of DVM distinguishing between the multiple groups or species within (and across) different layers. In the Atlantic, it was found that multiple densely populated layers were mainly due to different species of fish and cephalopods having distinct DVM behaviours [6]. In contrast, multiple dense layers in the St-Lawrence were due only to krill [5] that could switch between the different layers, suggesting that they had the same fitness in all these layers, possibly because of the presence of different prey (as it is the case for fish in our study). Organisms from very similar species can have different migration strategies [33], and organisms from the same species can have completely different DVM patterns—e.g. normal and reverse—in the coastal or open ocean [34]. Also, while many copepods migrate, a substantial proportion of the community can remain resident at depth day and night, for example in the North East Atlantic [35] or in the Irish Sea [34]. A common rule validated by our study is that bigger organisms migrate deeper [3, 33, 34] and that the large organisms usually do not migrate at all [33, 34]—even though the contrary is possible [36].

The biggest copepods, resident at depth, require a resource at depth to be able to survive. We hypothesised that this resource is a flux of detritus produced by the discard of the overlaying zooplankton community. While other non-modelled sources of food (extra zooplankton, benthic organisms in shallow water columns) might also play a role, our modelled particle flux is sufficient to support these big copepods at depth. In this, the coagulation process by which small detrital particles coalesce into larger faster sinking particles was an important factor to provide a sufficient flux to fuel the residency of the biggest copepods at depth. Model runs where this process was not included failed to replicate the non-migratory deep-residence of large copepod (cf. sensitivity analysis of the depth-dependent detritus preference function in the supplementary material) suggesting that their migration patterns may be substantially different in areas where detritus does not coagulate or where it gets broken down quickly.

An important feature highlighted by this study is that trophic interactions can lead to distinctly different

DVM patterns for different organisms within the same water column, providing a possible explanation for the multi-modal distributions that are consistently observed in the world ocean basins [1], but also for singular patterns such as reverse migrations. Our study focused on a few oceanic conditions where size-dependent DVM patterns are known, but we believe that provided with the correct set of environmental parameters the model could very well reproduce other patterns, and they should be investigated more systematically. For example, if the largest copepods consistently remain at depth, global estimates of DVM-mediated carbon exports could be very biased if the entire community is thought to behave alike (such as in [10]). In a context of global change where copepods are likely to become smaller in general [37–39], our model indicates that active carbon exports by migrating copepods could decrease if the abundance of intermediate-sized copepods migrating vertically decreases as well. But many other factors have to be taken into account (such as higher metabolism at increased temperatures), and the future of active carbon transport by zooplanktonic migrants remains uncertain [40, 41].

Trait-dependent DVM

Size is often recognised as a master trait [42], governing the main vital rates of organisms [43] as well as trophic interactions, and thus greatly influencing DVM patterns of plankton.

In addition to size, feeding mode shapes trade-offs that are different enough to trigger very different behaviours (figure 3); while active feeding copepods migrate, passive (i.e. ambush) feeding copepods remain resident at the surface. We are not aware of any study that looked specifically at the relation between DVM and feeding mode, but a few studies investigating DVM patterns at the species level corroborate our findings [33, 34, 44]: active copepods predominantly perform DVM, while ambush copepods tend to remain resident at a particular depth. In areas where a particular species dominates (active or passive feeder) this difference could cause very different migratory patterns at the community level, impacting in turn the magnitude of the biological pump.

Further, male and female copepods seem to have a different behaviour [35]. It is unclear if this difference is only due to a significant size difference between males and females changing their respective trade-offs, or if the trade-off itself is different irrespective of size, for example because of different reproductive investments. In many calanoid species, males feed less than females (or not at all) [45] and can thus remain deeper. In egg-carrying species, females do not risk only their own lives but also their offspring's, and seem to remain deeper than the individuals without eggs [46].

Traits and trait-based approaches are proving more and more useful to solve complex issues in marine ecosystems [42]. Predator-prey interactions often occur between many different species simultaneously, and trait-based approaches can be particularly useful in these cases as they can reduce the system complexity significantly. For example, trait-based approaches allow drawing conclusions on predator-prey interactions in little-studied ecosystems such as fresh waters [47], considering complex feeding interactions between marine mammals and many different prey species [48], predicting the outcome of potential invasive species in coral reefs [49], as well as estimating

ecosystem functions at an oceanic scale [50].

The role of light and proxies of DVM

Light levels are of great importance for the depth distribution of organisms in the water column [51], but the underlying mechanism is quite uncertain [52, 53]. Several studies explored the role of light in triggering DVM, mostly through the isolume hypothesis: zooplankton always remain at a constant light level [53]. However, studies considering this hypothesis only partially validate it, either because zooplankton follow the isolume only during part of the day [52] since they cannot keep up with a rapid change in light intensity [54], or because only organisms of particular stages and species follow an isolume [55]. The isolume hypothesis also fails to explain the quick response of zooplankton to the presence of predators in the water column [56], the emergence of reverse migration patterns, or even the presence of complete residency at certain depths. While light is a very important driver of DVM [53], and can be an important sensory proxy for migrating animals, it cannot be considered its only driver without oversimplifying the DVM process.

Variations in the light attenuation coefficient alone could not explain the differences between the five environmental scenarios from the California Current. A combination of different factors such as productivity and mixed layer depth is important when it comes to understanding the observed patterns. For high food abundance for instance, copepods can reduce their foraging time or feed in somewhat deeper waters, reducing their presence in light waters and thus their mortality risk. Abundance of food reduces the need for DVM. Our study emphasises the importance of prey and predator abundance as drivers of DVM patterns, but a justification on how organisms effectively sense and react to such abundance changes remains to be found.

Alternative defence mechanisms for pelagic organisms

While DVM is a key defence mechanism against predation in the pelagic, alternative defence strategies also exist. For example, schooling is seen as a way to decrease predation risk [57], and can thus be understood as a potential way to overcome the need for DVM. Schooling behaviours can also be adopted in complement to DVM, and often depend on the period of the day. Fish tend to disaggregate at night [58, 59], sometimes in concert with an upward migration [59]. However, schooling is not always an appropriate strategy, as it can also attract predators and increase predation pressure [60]. But this very fact may also attract the predator's predator, a process known as indirect trophic interaction. Piscivorous fish have been reported to patrol within krill swarms, on the look-out for potential planktivorous fish attracted by the swarms [61]. Here, the krill strategy can be compared with a strategy of reverse diel vertical migration: in both cases, the association with a dangerous area or species for predators offers some protection against them.

Moreover, we consider only two periods during a day: daytime and night-time. But light levels between these two periods vary smoothly, and this can provide fish with an extra incentive to change their distribution during transitions between day and night. Transition periods are risky for copepods whose visibility would suddenly

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increase if they do not time their ascent or descent optimally with light levels. Feeding rates increase tremendously at dawn and dusk [31], and for some fish up to 90% of the feeding has been found to take place during these transition times [62].Thus, bigger copepods suffer a higher mortality risk at dawn and at dusk than smaller ones, and the smaller copepods spend significantly more time at the surface than their bigger counterparts [63]. We decided not to include this extra complexity in the model, as it would increase computation time tremendously.

While DVM is one strategy that seeks to balance feeding opportunity with risk, other strategies, often used in concert with DVM, are also found. For instance, as visual predation is a main driver of copepod DVM, organism transparency can offset part of the risk of feeding at the surface. This is a strategy followed by some otherwise transparent species which migrate in tune to their gut fullness; digesting a meal at depth and returning to the surface to feed with an empty gut [52, 64]. Alternatively, some zooplankton species are adapted to survive in low oxygen conditions. Indeed, OMZs (Oxygen Minimum Zones, zones depleted of oxygen where most fish cannot survive for long [65]) are present in some marine ecosystems, primarily in upwelling regions. Copepods adapted to low oxygen conditions can take refuge in OMZs shallower than their "normal" migration depths [4, 66], thus remaining inaccessible to predators non-adapted to low oxygen conditions while shortening their DVM amplitude. This can explain why our copepod distributions in the clearest environmental scenarios (1–2) are more spread than observed in the California Current [4, 8]. Being in cold waters at depth also reduces metabolism [67] and is thus a way to increase fitness [68]. The internal state of a copepod can also be an incentive to migrate or not: a starving organism may be willing to face more risk and go closer to the surface than one with a full stomach, or additionally, an organism with a full gut would be more conspicuous to a visual predator than one with an empty gut. This idea gave rise to the foray hypothesis [69]: if a copepod already has a full stomach there is no benefit in staying at the surface. The migration patterns of an individual then depend on the time it takes the individual to fill and empty its stomach, and will consist of many ascents to feeding areas followed by descents into safe depths as soon as its stomach is full.

Conclusion

Using game theory, we have shown that DVM patterns of zooplankton and planktivorous fish do not depend only on light levels and environment conditions but also on the structure of the pelagic food-web. Within a single framework, we provide an explanation for the wide variety of migratory patterns observed in nature, including multi-modal distributions and reverse migrations [1, 26]. To our knowledge, this is the first time that a model provides such an explanation, and the first time that a model provides DVM patterns for so many different organisms at the same time. It shows the importance of considering trophic interactions when modelling DVM in general.

Understanding and quantifying the drivers of vertical migratory behaviours under different oceanic conditions is vital as it can lead to more precise estimates of DVM patterns worldwide, and of carbon actively transported to the depths by migrating organisms, which can be a substantial part of the carbon pump [10, 12]. It is clear

from this work that all aspects of the marine food-web are implicated in this active transport, not just as primary agents but also in setting the environmental parameters which govern DVM and its associated flux. How climate change will affect the emergent community structure of marine ecosystems and its cascading effects for the active carbon flux remains an important question for Earth system research.

Data, code and material

The source code (written in MATLAB) supporting this article has been uploaded as part of the supplementary material.

Competing interests

The authors declare to have no conflict of interest.

Author's contributions

J.P., T.K. and A.W.V designed the study; J.P. conceptualized the model with help from U.H.T. and A.W.V.; J.P. coded the model; J.P. analyzed the results with the help of all authors. J.P. wrote the paper with contributions from all authors.

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