Evaluating the Potential Impacts of the Diurnal Vertical Migration by Marine Organisms on Marine Biogeochemistry

Olivier Aumont, Olivier Maury, Stelly Lefort, Laurent Bopp

To cite this version:

Olivier Aumont, Olivier Maury, Stelly Lefort, Laurent Bopp. Evaluating the Potential Impacts of the Diurnal Vertical Migration by Marine Organisms on Marine Biogeochemistry. Global Biogeochemical Cycles, 2018, 32 (11), pp.1622-1643. 10.1029/2018GB005886 . hal-01994134

AGU100 ADVANCING EARTH AND SPACE SCIENCE

Global Biogeochemical Cycles

RESEARCH ARTICLE

10.1029/2018GB005886

Key Points:

- First global end-to-end ecosystem model that explicitly represents migrating organisms
- Active flux of carbon due to DVM amounts to 18% of the passive flux due to sinking particles
- Total impact on oxygen in the mesopelagic domain is modest

Correspondence to:
O. Aumont,
olivier.aumont@ird.fr

Citation:
Aumont, O., Maury, O., Lefort, S., & Bopp, L. (2018). Evaluating the potential impacts of the diurnal vertical migration by marine organisms on marine biogeochemistry. *Global Biogeochemical Cycles*, *32*, 1622–1643. https://doi.org/10.1029/2018GB005886

Received 15 JAN 2018
Accepted 11 OCT 2018
Accepted article online 15 OCT 2018
Published online 8 NOV 2018

Evaluating the Potential Impacts of the Diurnal Vertical Migration by Marine Organisms on Marine Biogeochemistry

Olivier Aumont[1], **Olivier Maury**[2], **Stelly Lefort**[3], **and Laurent Bopp**[4]

[1]Laboratoire d'Océanographie et du Climat: Expérimentations et Approches Numériques (LOCEAN), IRD-IPSL, Paris, France, [2]IRD (Institut de Recherche pour le Développement), UMR 248, MARBEC, Sète, France, [3]Laboratoire des Sciences du Climat et de l'Environnement (LSCE), IPSL, CEA–Orme des Merisiers, Gif-sur-Yvette, France, [4]Laboratoire de Météorologie Dynamique, Ecole Normale Supérieure-PSL Res. Univ., CNRS, Sorbonne Université, Ecole Polytechnique, Paris, France

Abstract Diurnal vertical migration (DVM) of marine organisms is an ubiquitous phenomenon in the ocean that generates an active vertical transport of organic matter. However, the magnitude and consequences of this flux are largely unknown and are currently overlooked in ocean biogeochemical models. Here we present a global model of pelagic ecosystems based on the ocean biogeochemical model NEMO-PISCES that is fully coupled to the upper trophic levels model Apex Predators ECOSystem Model, which includes an explicit description of migrating organisms. Evaluation of the model behavior proved to be challenging due to the scarcity of suitable observations. Nevertheless, the model appears to be able to simulate approximately both the migration depth and the relative biomass of migrating organisms. About one third of the epipelagic biomass is predicted to perform DVM. The flux of carbon driven by DVM is estimated to be 1.05 ± 0.15 PgC/year, about 18% of the passive flux of carbon due to sinking particles at 150 m. Comparison with local studies suggests that the model captures the correct magnitude of this flux. Oxygen is decreased in the mesopelagic domain by about 5 mmol m^{-3} relative to simulations of an ocean without DVM. Our study concludes that DVM drives a significant and very efficient flux of carbon to the mesopelagic domain, similar in magnitude to the transport of DOC. Relative to a model run without DVM, the consequences of this flux seem to be quite modest on oxygen, due to compensating effects between DVM and passive fluxes.

1. Introduction

Diurnal vertical migrations (DVM) by zooplankton and micronekton are a widespread phenomenon in marine environment. Typically, migrating organisms are staying at the surface at night and descend to depth at dawn. At sunset, they return to the surface to feed on epipelagic preys. The vertical amplitude of these movements may reach several hundreds of meters. Numerous observations, such as acoustic surveys, have evidenced regular DVM and demonstrated that they are ubiquitous across a wide range of ecological provinces (Banse, 1964; Luo et al., 2000; Steinberg, Cope, et al., 2008). However, the existence of inverted temporal sequences of DVM (at the surface during daytime and at depth during nighttime) or desynchronized vertical movements has also been observed in polar regions (Cohen & Forward, 2009; Neill, 1990).

Several mechanisms have been proposed to explain the existence of DVM. DVM are energetically a cost for migrating organisms because they are spatially separated during the day from their epipelagic preys so that they cannot feed at maximal rates. Furthermore, colder waters in the mesopelagic domain reduce their reproductive and growth fitness (Aksnes & Giske, 1990; Dawidowicz & Loose, 1992; Pangle & Peacor, 2006). Thus, there must be some benefit of descending at depth. The most likely benefit of DVM is the so-called predator evasion hypothesis (e.g., Lampert, 1989; Zaret & Suffern, 1976): Migrants descend at depth during daytime to escape predation by visual predators. The mesopelagic domain is thus used as a dark refuge. This explanation may also be used to explain the reverse DVM temporal patterns in that zooplanktonic organisms may swim at depth to avoid filter-feeding invertebrate organisms such as jellyfish (Ohman et al., 1983). One of the most compelling evidence for the role of predation in driving DVM is the observation that zooplankton alters the amplitude of their vertical movements in response to the presence of planktivorous fish or fish kairomones (e.g., Bollens et al., 1995; Loose et al., 1993; Ringelberg & Gool, 2003). Another potential cause of DVM is the damaging effect of sunlight, especially UV, which has been one of the earliest proposed explanations (Moore, 1912).

DVM influence the ecology of the upper ocean by altering the predation patterns, both in time and space (Hays, 2003). Furthermore, they have an impact on the vertical fluxes of carbon, nutrients and oxygen. Migrating organisms feed only at the surface, but they respire, excrete, produce fecal pellets, and can be grazed both at the surface and in their deep habitat. As a consequence, vertically migrating organisms are responsible for an active flux of carbon and nutrients from the surface to the mesopelagic domain. It has been suggested that this active transport could enhance the efficiency of the biological pump (e.g., Buesseler & Boyd, 2009). It is all the most efficient because, unlike passive export by sinking particles, active export escapes intense remineralization in the upper layers of the ocean. It induces thus a flux to the depth at which migrating organisms reside during daytime, which could be at several hundreds of meters.

The passive flux of carbon is usually studied in the field using sediment traps at various depth, thorium desequilibration technique, and/or underwater imaging systems (e.g., Falkowski et al., 2003; Guidi et al., 2008; Henson et al., 2011). Because these measurement techniques do not sample active flux by migrants, most estimates of export production ignore active transport and are therefore likely to underestimate the total export of carbon and nutrients to the mesopelagic domain. It should be noted here that an additional component of the biological pump, the transport of DOC by the ocean dynamics, is also not sampled by these measurement techniques (Hansell & Carlson, 2001; Hansell et al., 2009). The active component of the biological pump is still poorly quantified, especially with respect to the passive export by sinking particles. Field studies suggest that this component could represent between 10% and 50% of the total export of carbon to the ocean's interior (Emerson et al., 1997; Hernández-León et al., 2001; Isla et al., 2015; Packard & Gómez, 2013; Steinberg, Cope, et al., 2008). However, these studies often neglect or underestimate the role of micronekton due to its low capture efficiency, despite its potentially large contribution to the total active flux (Davison et al., 2013; Kaartvedt et al., 2012).

Modeling studies have mainly focused on the characteristics of DVM in response to various stimuli such as light, predation, and food abundance. These mathematical models generally rely on a trade-off between predator avoidance and food consumption. Two different theoretical approaches have been used to model DVM. Some models are based on some elements of game theory where organisms choose between different strategies based on a payoff matrix (Gabriel & Thomas, 1988; Sainmont et al., 2013). The other type of models assumes that migrating organisms should maximize some fitness function such as reproduction or the ratio of energy gain over mortality (De Robertis, 2002; Enright, 1977; Fiksen & Carlotti, 1998). Thus, most of these models rely on the optimization of a fitness function whose choice and formulation remain uncertain and then, partly subjective. In a recent study (Morozov & Kuzenkov, 2016), a general framework of DVM based on the selection of the fittest organisms in an infinite space of strategies has been developed to overcome this shortcoming. However, these modeling studies have been performed in idealized setups and do not address the effects of DVM on marine biogeochemistry and ecology. To our knowledge, only one modeling study has studied the biogeochemical and ecological consequences of DVM at three 1-D stations located in the Pacific Ocean (Bianchi, Stock, et al., 2013). In a parallel study, Bianchi, Galbraith, et al. (2013) have estimated the impact of DVM on oxygen at the global scale, but without explicitly modeling migrating organisms.

In the present study, we use a fully coupled modeling framework which represents the whole pelagic ecosystem. This modeling framework is based on the NEMO system to predict ocean dynamics (Madec, 2008), PISCES to describe marine biogeochemistry and the lower trophic levels (phytoplankton and zooplankton; Aumont et al., 2015), and Apex Predators ECOSystem Model (APECOSM) to simulate the upper trophic levels (large mesozooplankton to fish; Maury, 2010; Maury et al., 2007). PISCES and APECOSM are fully coupled which means that they exchange information in a bi-directional manner and that the nutrients and carbon cycles are closed. NEMO-PISCES-APECOSM (hereafter called NPA) can thus be considered as an end-to-end ecosystem model (Fulton, 2010; Rose et al., 2010). It is, to our knowledge, the first global-scale end-to-end ecosystem model in which all trophic levels (from primary producers to top predators) fully interact. APECOSM includes three generic communities of which one corresponds to organisms performing DVM. Thus, this makes NPA suitable to study the impacts of DVM on marine ecosystems and biogeochemistry.

Our objectives here are threefold: (1) Evaluate the ability of NPA to simulate the major characteristics of DVM, (2) estimate the magnitude and spatial patterns of the active fluxes of carbon driven by DVM, and

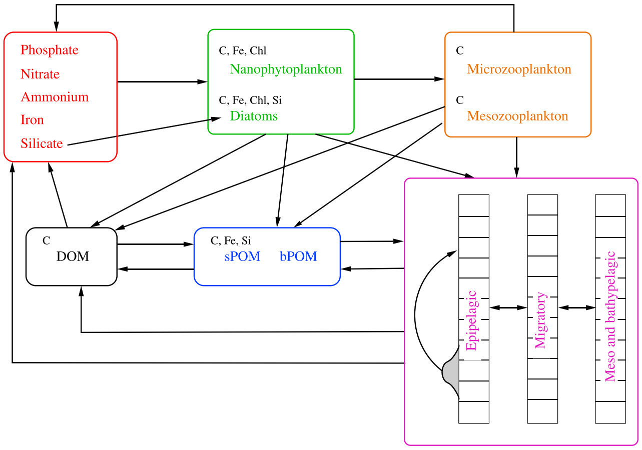

Figure 1. The biogeochemical model PISCES-APECOSM. DOM stands for dissolved organic matter and POM for particulate organic matter.

(3) investigate the impacts of DVM on marine global biogeochemistry, and more specifically on oxygen. The rest of the paper is organized as follows: Section 2 describes the NPA modeling framework, with a special emphasis on the description of DVM in APECOSM. Section 3 evaluates the model behavior and estimates the magnitude of the active fluxes of carbon. Section 4 discusses the model caveats and the consequences of DVM on marine biogeochemistry, especially oxygen distribution and carbon fluxes. In the last section, we conclude the paper.

2. Methods

2.1. Models

In this study, we use the coupled model NEMO-PISCES-APECOSM. Ocean dynamics and the transport of all active and passive prognostic tracers are simulated by the Ocean General Circulation Model NEMO (Madec, 2008). The PISCES model is embedded in NEMO. It represents marine biogeochemistry and lower trophic levels, including four plankton functional types (Aumont et al., 2015). The upper trophic levels are simulated by APECOSM, based on three size-structured generic marine pelagic communities (Maury, 2010; Maury et al., 2007). The NEMO-PISCES model configuration is identical to that of Aumont et al. (2015). The PISCES-APECOSM coupling is similar to that of Lefort et al. (2015) and Le Mézo et al. (2016). However, in these previous studies, there was no feedback from APECOSM to PISCES (one-way coupling). Here upper trophic levels impact on lower trophic levels and marine biogeochemistry through predation, respiration, excretion, and egestion (two-way coupling). A schematic diagram of PISCES-APECOSM is presented in Figure 1. The parameters of APECOSM have been modified relative to their standard original values (Maury et al., 2007) to produce realistic fields of both for low and high trophic levels (Table 1).

2.1.1. NEMO-PISCES

The dynamic state of the ocean has been simulated using the ORCA2-LIM configuration of the NEMO modeling platform in version 8.2 (Madec, 2008). It consists of the ocean general circulation model OPA9 coupled to the dynamic-thermodynamic Louvain-la-Neuve ice model (LIM2) (Timmermann et al., 2005). The ORCA2 domain configuration has approximately 2° horizontal resolution in the extratropics, with meridional resolution increasing to 0.5° at the equator. The ocean model includes 30 vertical levels, with 20 of these in the upper 500 m. Representation of the topography is based on the partial-step thicknesses (Barnier et al., 2006). Lateral mixing is oriented along isopycnal surfaces, and the parameterization of Gent and McWilliams (1990) for sub-grid-scale processes is used poleward of 10° latitude in both hemispheres. For vertical mixing, the turbulent kinetic energy scheme of Blanke and Delecluse (1993) is used. The dynamics used to drive PISCES and APECOSM is identical to that used in Aumont et al. (2015).

The marine biogeochemical model PISCES-v2 (Aumont et al., 2015) is part of the NEMO modeling framework. PISCES simulates the sources and sinks of 24 prognostic variables. The low trophic levels are described by two phytoplankton groups (nanophytoplankton and diatoms) and two zooplankton size classes

Table 1
Main Parameters of NPA That Have Been Changed Compared to the Initially Published Values

Parameter	Units	Value	Description
m^M	$(\mu\text{mol C L}^{-1})^{-1}$	0.005	Mesozooplankton quadratic mortality
ω	$\text{kg}\cdot\text{kg}^{-2/3}\cdot\text{s}^{-1}$	2.28×10^{-7}	Maximum surface specific ingestion rate
μ	$\text{J}\cdot\text{kg}^{-1}\cdot\text{s}^{-1}$	0.07	Maintenance rate
C	J/m^3	400, 133	Holling type II half-saturation constant (nonvisual, visual)
τ_A	K	6000	Arrhenius temperature-dependent correction factor
ρ	–	8	Optimum predator:prey radius ratio
σ	–	1.0	Standard deviation of log of preference
L_r	W/m^2	10^{-4}	Preferred isolume of the migratory OOPC
σ_L	–	0.75	Standard deviation of log of preferred isolume

Note. NPA = NEMO-PISCES-APECOSM; OOPC = Open Ocean Pelagic Community.

(microzooplankton and mesozooplankton). Phytoplankton growth is controlled by five limiting nutrients (Fe, PO_4, $Si(OH)_4$, NO_3, and NH_4) in addition to light and temperature. There are three nonliving compartments in PISCES corresponding to semilabile dissolved organic matter and two size classes of particulate organic matter (POM) which differ by their size (1–100 μm for small particles and 100–5000 μm for large particles) and their sinking speed. The stoichiometry of organic matter for N, P, and C is fixed and set to values proposed by Takahashi et al. (1985). The ratios of both Si and Fe to C are variable and modeled prognostically. Oxygen is computed from the different sources and sinks (such as photosynthesis, nitrification, and respiration) assuming constant ratios as detailed in Aumont et al. (2015). Below a certain oxygen concentration, set to 6 μmol/L, remineralization of organic matter progressively switches to denitrification. Degradation of organic matter occurs through denitrification only below 1 μmol/L. The configuration of PISCES-v2 used here is almost exactly identical to that of Aumont et al. (2015) including the values of the model parameters. Nevertheless, since predation by the upper trophic levels is now explicitly represented in APECOSM, the quadratic mortality parameter of mesozooplankton has been strongly reduced from its standard value of 0.03 $(\mu\text{mol C L}^{-1})^{-1}$ day^{-1} to 0.005 $(\mu\text{mol C L}^{-1})^{-1}$ day^{-1} (Table 1). The mesozooplankton compartment of PISCES is not assumed to perform vertical migrations.

2.1.2. APECOSM

The APECOSM represents the flow of energy through the ecosystem with a size-resolved structure in both 3-D space and time (Maury, 2010; Maury et al., 2007). This flow of energy is controlled by opportunistic predation, which depends on the size ratio between the predators and the preys, and by organisms' growth. Here the selectivity function describing the size preference for prey is prescribed with a normalized lognormal function (Anderson & Ursin, 1977; Hartvig et al., 2011). It produces more stable size spectra than the original selectivity function used in APECOSM, which was relatively similar to a rectangular shape function (Datta et al., 2011). The allocation of energy for growth and reproduction is based on the Dynamic Energy Budget theory (Kooijman, 2009). A fixed fraction of the assimilated energy is allocated to growth and somatic maintenance, the rest being devoted to eggs production and maturity maintenance. Eggs production is continuous in time and is routed to the beginning of the size spectrum as a Neumann condition. In addition to predation, organisms experience nonpredatory losses (both linear and quadratic) and starvation mortality. All the physiological rates are temperature dependent. Both active and passive movements are taken into account (Faugeras & Maury, 2007). The 3-D fields of phytoplankton, zooplankton, and POM simulated by PISCES fuel the interactive communities represented in APECOSM, which in turn exerts a predation mortality on the low trophic levels (two-way coupling) in contrast to the modeling framework (one-way coupling) used in Lefort et al. (2015) and Le Mézo et al. (2016). Egestion, respiration and excretion by the upper trophic levels are routed to the appropriate organic and inorganic compartments of PISCES (i.e., DIC, NH_4, POM, and dissolved organic matter). As a result, NPA rigorously conserves mass.

Upper trophic levels in APECOSM are split into three distinct communities: The epipelagic Open Ocean Pelagic Community (OOPC), which is located in the upper ocean, mostly in the first 200 m of the ocean; the mesopelagic and bathypelagic OOPC, which inhabits the mesopelagic and bathypelagic domain of the ocean; and the migratory OOPC, which performs diurnal vertical migration between the epipelagic and the mesopelagic domains. Each OOPC is ranging from 1 mm to 2 m in size, discretized into 20 size classes evenly distributed on a logarithmic size axis. The epipelagic community includes visual predators and filter feeders. These two groups are not explicitly distinguished, but visual feeders are accounted for by assuming that they can reach full satiety with 3 times less food than filter feeders and that they cannot feed at night (Kiørboe, 2011). Their relative contribution to the epipelagic community is computed by making the (strong) assumption of instantaneous equilibrium between visual and filter feeders contributions. In that case, the ratio between visual and nonvisual feeders is equal to the ratio of their growth rates which can be easily computed at each time step.

The resident mesopelagic community is supposed to feed both day and night. The visual feeding epipelagic community can feed only during daytime when there is sufficient light, whereas the filter-feeding epipelagic organisms can feed all day long. The migrating organisms are assumed to use a nonvisual strategy for predation. Furthermore, we make the hypothesis that they feed during only part of the day, that is, when they reside in the epipelagic domain (during night time). This is the only penalty assumed to be experienced by these organisms in our model setup. The vertical habitat of the three OOPCS is constrained by light, food, and oxygen (Maury, 2010). Fecal pellet production performed by the organisms that feed only during part of the day is supposed to be a constant fraction of the total amount of food that has been ingested during the feeding period. It is then distributed over the whole day as a function of their habitats, the time they spend in these habitats, and the temperature experienced. Thus, fecal pellet production is continuous and continues even when the organisms are not feeding anymore.

Since the primary focus of this study is diurnal vertical migration, we describe more extensively the migratory OOPC here. It is generally accepted that light is the primary proximate control cue that controls both the timing and the amplitude of the DVM (Cohen & Forward, 2009; Ringelberg, 1995). A hypothesis that has received considerable attention is the light preferendum hypothesis, which postulates that vertically migrating organisms remain within a preferred light domain (Aksnes et al., 2017; Cohen & Forward, 2009; Frank & Widder, 2002). Following, we assume in APECOSM that migratory organisms cluster around a defined isolume:

$$H(L) = \exp\left(-\frac{\left(\log(L) - \log(L_r)\right)^2}{\sigma_L^2}\right) \tag{1}$$

where L is the local light level, L_r is the preferred isolume, and σ_L^2 is the variance of the distribution. Based on quick comparisons with acoustic data, L_r and σ_L have been set to respectively 10^{-4} W/m^2 and 0.75. This value for the preferred light level is significantly higher than what has been estimated from acoustic data by Aksnes et al. (2017), around 10^{-7} W/m^2. Improper representation of light attenuation below the upper ocean may explain this bias in our model. During nighttime, the distribution of the migrating community is supposed to be identical to that of the resident epipelagic community, which is mainly a function of food abundance.

Using an array of backscatter data, Bianchi, Galbraith, et al. (2013) have shown that oxygen is an even better predictor than light of DVM daytime depth and have proposed a global empirical relationship that predicts DVM depth as a function of the vertical gradient in oxygen and temperature, surface chlorophyll, and the mixed layer depth. Unfortunately, this relationship cannot be used in APECOSM as it predicts that migratory organisms descend in the core of oxygen minimum zones (OMZs) where oxygen levels are insufficient to sustain respiration of these organisms (in that case, the model would predict negative oxygen concentrations). With our parameterization, that problem may still occur since the preferred isolume may fall within the core OMZ. Thus, we impose a minimum threshold on O_2 below which migratory organisms cannot reside. Accordingly, the vertical habitat predicted by equation (1) is altered so that organisms descend to the vertical level located immediately above that threshold, which has been set to an oxygen concentration of 10 μmol/L.

Vertical movements performed by migrating organisms while they move up and down in the water column are extremely rapid, typically a few centimeters per second (Bianchi & Mislan, 2016; Heywood, 1996; Jiang et al., 2007), much larger than the vertical dynamical velocities, which are several orders of magnitude smaller. An explicit resolution of the vertical movements would require very small time steps to respect the Courant-Friedrichs-Lewy criterion (Courant et al., 1928), a few minutes given the vertical resolution of our model, to be compared with an actual time step of 3 hr. Instead, vertical migrations are assumed to be instantaneous. As a consequence, migratory organisms move instantaneously between their daytime and nighttime habitats at sunset and sunrise. At high latitudes, when daytime period exceeds 18 hr, organisms are assumed to performed unsynchronized vertical movements (i.e., independently of the daytime and not all at once; e.g., Blachowiak-Samolyk et al., 2006; Cottier et al., 2006). We further make the assumption that they stay at the surface for 6 hr. In the opposite situation, when nighttime period exceeds 18 hr, synchronized migrations are prescribed to continue with a residence time at depth set to 6 hr (Berge et al., 2009, 2012). Since light levels are extremely low in that case, the habitat depth cannot be determined from equation (1) as it would be located at the surface and is arbitrarily prescribed at 350 m.

2.2. Model Experiments

In this study, we use an *offline* version of NPA in which the model is forced by outputs from the ocean dynamical simulation. The model setup as well as the ocean dynamical fields are identical to those of Aumont et al. (2015). In a first step, the model has been run in a *one-way* coupling configuration for 300 years until the OOPCs simulated by APECOSM reach a quasi steady state. During this first spin-up phase, PISCES has been initialized from the simulation presented in Aumont et al. (2015) and OOPCs in APECOSM have been set to very small values. Then, at the end of this first phase, the *two-way* coupling mode has been activated and the model has been run for an additional 1,000 years. After that duration, all biogeochemical and biological fields have reached a stationary solution.

In addition to that standard simulation, we have performed an additional sensitivity experiment to evaluate the impact of DVM on the simulated ocean biogeochemistry. In that experiment, migratory organisms still perform their vertical migrations so that their impact on the marine ecosystem through predation is conserved. However, the products that they would normally excrete, respire, and egest in deep waters during daytime are released close to the surface according to their nocturnal habitat. Thus, the active transport of carbon, nutrients and organic matter is virtually set to 0. This additional experiment `NoMig` has been initialized from the first spin-up phase and has been run, as for the standard simulation `Std`, for 1,000 years.

2.3. Observations

The simulated model biomass are evaluated against databases of mesozooplankton (0.2 – 2 mm) and macrozooplankton (2 mm to 2 cm) assembled by the MAREDAT initiative (Buitenhuis et al., 2013). The mesozooplankton MAREDAT database (Moriarty & O'Brien, 2013) has been constructed from the Coastal and Oceanic Plankton Ecology, Production, and Observation Database (COPEPOD, http://www.st.nmfs.noaa.gov/copepod), a project of the U.S. National Marine Fisheries Service. After a rigorous quality control, 153,163 biomass values have been converted from their original units to carbon biomass. Data were binned then on the traditional four-dimensional World Ocean Atlas (WOA) grid (1° horizontal resolution with 33 vertical levels) and cover about 20% of the surface of the ocean. The macrozooplankton database (Moriarty et al., 2013) has been assembled from four existing databases. After quality control, this database contains 280,631 nonzero abundance data points (in ind L^{-1}), which cover large parts of the ocean with the exception of the tropical and temperate South Pacific and the tropical North Atlantic. As for mesozooplankton, the data points have been binned on the WOA grid.

In addition to these two databases, we have also used the original COPEPOD database to attempt to estimate the contribution of migratory organisms to the total biomass in the epipelagic domain. For each cruise stored in the database, we have binned the daytime and nighttime epipelagic biomass data points on the traditional three-dimensional WOA grid. Then, for each cruise, the nighttime to daytime biomass ratio has been computed for each grid cell in which that was possible. Finally, the median of the computed ratios has been computed when several cruises had sampled the same grid cell. The 1,307 ratios can be computed using that procedure. This method is subject to strong potential biases. Day-night biomass differences may reflect daytime net avoidance (Zhang & Dam, 1997). They may also arise from the high spatial and temporal variability of zooplankton and micronekton (Barange, 1994; Piontkovski & Williams, 1995; Stupnikova & Vereshchaka, 2013). Furthermore, net sampling is characterized by potentially high biomass losses due to the evasion of larger swimmers (Kaartvedt et al., 2012; Koslow et al., 1997) even if that should alter in a similar manner the sampling of migrating and nonmigrating organisms.

A survey of the published literature enabled the creation of a data set of the contribution of migratory organisms to the total epipelagic biomass. We only retained the studies specifically dedicated to diurnal vertical migrations. A large number of published studies were not considered in our survey because they were either focusing on specific species or groups (e.g., copepods or euphausiids) or because the data were displayed in such a manner that computation of the contribution of migratory organisms was impossible. Most of the available observations concern mesozooplankton and/or micronekton, such that in the database, only very few data points refer to the whole community. References from which the database is derived are as follows: Rodier and Le Borgne (1997); Yamaguchi et al. (2002); Smeti et al. (2015); Haury et al. (2000); Cook et al. (2013); Head et al. (1999); Allison and Wishner (1986); Madhupratap et al. (2001); Décima et al. (2016); Yebra et al. (2009); Putzeys et al. (2011); Roman et al. (2002); Le Borgne et al. (2003); Martin and Christiansen (2009); Décima et al. (2011); Hays, Harris, et al. (2001); Hernández-León et al. (2001); Steinberg, Cope, et al. (2008); Dam et al. (1995); Champalbert et al. (2005); Champalbert et al. (2003); Kitamura et al. (2016); Landry et al. (2001); Hidaka et al. (2001); Madin et al. (2001); Timonin (1995); Pal et al. (2010); Marlowe and Miller (1975); Smith et al. (1998); Perissinotto and McQuaid (1992); Inoue et al. (2016); Hopkins (1982); Ward et al. (1995). The database includes 96 data points.

A similar survey has been performed for the active flux of carbon induced by DVM. As for the contribution of migratory organisms, most of the published studies focus on mesozooplankton and only very few include the contribution by large organisms such as fishes. References from which the database is derived are as follows: Yebra et al. (2009); Isla and Anadón (2004); Isla et al. (2015); Darnis and Fortier (2012); Dam et al. (1993, 1995); Kobari et al. (2013); Davison et al. (2013); Hidaka et al. (2001); Zhang and Dam (1997); Takahashi et al. (2009); Longhurst et al. (1989); Rodier and Le Borgne (1997); Hernández-León et al. (2001); Al-Mutairi and Landry (2001); Longhurst and Glen Harrison (1988); Steinberg et al. (2000); Stukel et al. (2013);

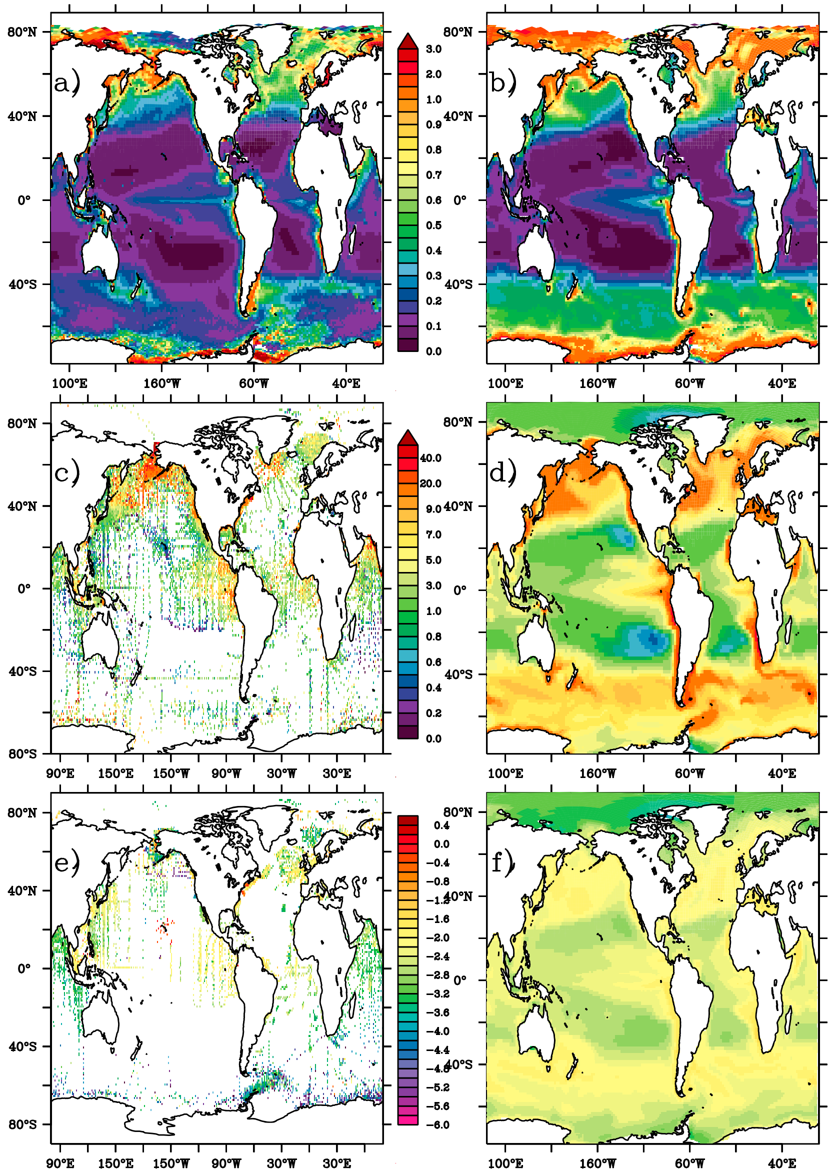

Figure 2. Evaluation of different living biomasses as simulated by PISCES-APECOSM. Panels (a) and (b), respectively, are GlobColour (1998–2012) estimates of surface chlorophyll and simulated surface chlorophyll in PISCES (in mg Chl/m^3); panels (c) and (d) are mesozooplankton biomass averaged between 0- and 150-m depths from the MAREDAT observations (1990s to 2012) and as predicted by PISCES-APECOSM, respectively (in μg C/L); (e) and (f) are observations of macrozooplankton abundance averaged over the first 150 m from MAREDAT observations (1990s to 2012) and as simulated by APECOSM, respectively (in L^{-1}). In the latter two panels, the decimal logarithm of the abundance is displayed. APECOSM = Apex Predators ECOSystem Model.

Escribano et al. (2009); Fernández-Urruzola et al. (2016). The database includes 33 data points. Obviously, none of these two databases based on literature surveys are considered to be exhaustive.

3. Results

3.1. Evaluation of Simulated Biomasses

Complete evaluation of the NPA model is beyond the scope of this study. However, we present a rapid evaluation of the main aspects of the model behavior. The evaluation of the upper trophic levels is rather difficult to achieve because of the limited number of available data. For size classes above a few centimeters, we are not aware of any database available in the literature. Figure 2 displays the annual-mean distribution of surface chlorophyll, mesozooplankton, and macrozooplankton averaged over the upper 150 m of the ocean.

Table 2
Statistical Comparison of the Two-Way Coupling and One-Way Coupling Configurations of NEMO-PISCES-APECOSM With the Observations for the Global Ocean

	Two-way coupling			One-way coupling		
Prognostic variables	*R*	RMSE	Bias	*R*	RMSE	Bias
Chlorophyll (mg Chl/m^3)	0.81	0.38	0.01	0.80	0.38	0.01
Mesozooplankton (μg C/L)	0.58	2.17	0.55	0.56	2.74	0.81
Macrozooplankton (#/m^3)	0.4	28.8	−2.0	0.37	30.6	-1.8

Note. *R* and RMSE are respectively the Pearson's correlation coefficient and the root-mean-square error. APECOSM = Apex Predators ECOSystem Model.

Surface chlorophyll concentrations are compared to GLOBCOLOUR satellite observations (http://globcolour.info). The observed patterns are qualitatively reproduced by the model. Predicted chlorophyll concentrations are too high in the eastern Pacific Ocean. This overestimation is not simulated in the standard version of PISCES-v2 (see; Aumont et al., 2015), which suggests that it might be due to the two-way coupling of PISCES with APECOSM. Indeed, grazing pressure by microzooplankton on phytoplankton is significantly decreased as a consequence of more intense predation by mesozooplankton and upper trophic levels on microzooplankton. In the Arabian Sea, chlorophyll concentrations are quite strongly underestimated. In that region, mesoscale and submesoscale activities have been shown to play a critical role to sustain biological production (Hood et al., 2003; Lee et al., 2000; Resplandy et al., 2011). In the Southern Ocean, the largest High-Nutrient-Low-Chlorophyll region, simulated chlorophyll levels appear to be quite strongly overestimated when compared to the GLOBCOLOUR satellite product. However, comparison of satellite-derived concentrations to in situ observations have evidenced that standard satellite algorithms used to retrieve chlorophyll from reflectance underestimate in situ observed values by a factor of about 2, especially at intermediate chlorophyll levels (Garcia et al., 2005; Kahru & Mitchell, 2010; Korb et al., 2004).

Mesozooplankton distribution is compared to observations from the MAREDAT database in Figures 2c and 2d (Moriarty & O'Brien, 2013). Mesozooplankton in NPA corresponds to the standard mesozooplankton compartment of PISCES plus the first two smallest size classes of the three communities modeled in APECOSM. The spatial patterns and orders of magnitude of the mesozooplankton biomass appears to be in qualitative agreement with the observations. However, the model underestimates the high biomass that is observed in the equatorial regions and in the high latitudes of the Northern Hemisphere, especially in the North Pacific Ocean. As a consequence, the spatial variations between the productive and oligotrophic areas appear to be less contrasted than suggested by the in situ data. Unfortunately, the seasonal variability of mesozooplankton cannot be properly evaluated because of the insufficient temporal coverage of the observations, except in very few regions such as the western and eastern coastal domains of the United States.

Both modeled and observed macrozooplankton distributions are displayed in Figures 2e and 2f. The model seems to be able to achieve a reasonable representation of the observed abundance of macrozooplankton (inferred from the number of organisms per liter). Nevertheless, assessing the model's predictions is impossible in wide regions of the global ocean where the spatial coverage of the data is insufficient such as in the entire South Pacific Ocean and the Tropical North Atlantic Ocean, for instance. Furthermore, as for mesozooplankton, the seasonal variability of macrozooplankton cannot be inferred from the observations. In the Southern Ocean, the model seems to strongly overestimate macrozooplankton abundance by up to 2 or 3 orders of magnitude, whereas it appears to quite underestimate the high biomass observed in some coastal areas such as along the eastern coast of the United States. Overall, the chlorophyll, mesozooplankton, and macrozooplankton distributions appear to be partly spatially correlated with similar regions exhibiting high and low biomass levels. However, the spatial contrasts tend to weaken as one moves up in the trophic food chain.

A more quantitative evaluation of the model behavior is presented in Table 2. As a comparison, the statistical scores are also presented for the one-way coupling configuration of the model. The scores for the two configurations of the model are relatively similar. Thus, the explicit feedback of the upper trophic levels on the lower trophic levels and marine biogeochemistry does not alter the model performance. The only large difference

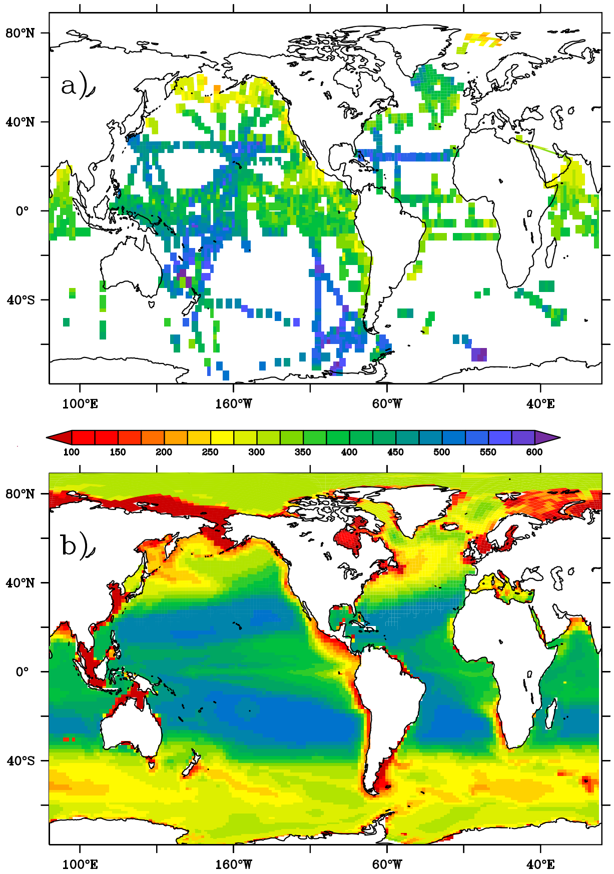

Figure 3. Annual-mean daytime DVM depths (m). (a) DVM depths derived from acoustic data binned on a 4° by 4° grid (Bianchi, Galbraith, et al., 2013), b) DVM depths predicted by APECOSM. DVM = diurnal vertical migration; APECOSM = Apex Predators ECOSystem Model.

between the two model configurations is the bias for mesozooplankton, which equals 0.55 and 0.81 μg C/L for the two-way and one-way coupling configurations, respectively. Thus, the mesozooplankton biomass in the former configuration is on average lower, which suggests a stronger control by the upper trophic levels. The simulated patterns of mesozooplankton and macrozooplankton are less well captured than chlorophyll since the correlation coefficients of these two zooplankton size classes are significantly lower.

3.2. Evaluation of the Horizontal and Vertical Distribution of the Migratory Community

In this section, we focus more specifically on the evaluation of the spatial patterns and biomass of the migratory community predicted by NPA. The depth at which migratory organisms dive during the day is of critical importance when evaluating the impact of DVM on ocean biogeochemistry: A deeper migration depth should produce a more efficient export of organic matter. Bianchi, Galbraith, et al. (2013) have constructed a global database of DVM depths from the analysis of acoustic Doppler current profilers collected during 389 cruises performed between 1990 and 2011. The depths of diel migration predicted by NPA are compared to the depths from that database in Figure 3. The most striking deficiency is simulated in regions characterized by intense OMZs, that is, the eastern equatorial Pacific, the Arabian Sea, and the Bay of Bengal. Studies with eddy resolving models have shown that this bias is explained by an unrealistic representation of the equatorial current system in coarse-resolution models (Dietze & Loeptien, 2013; Duteil et al., 2014). In these regions, the model predicts much too shallow depths of diel migration. Migratory organisms are assumed to be unable to stay in very anoxic waters (see section 2.1.2). In those waters, they would not be able to meet their respiration requirements unless negative oxygen concentrations are produced. In the database, DVM depths are quite deeper which suggests that migratory organisms descend to the core of the OMZs, probably to escape predation (Ekau et al., 2010; Wishner et al., 1995). Thus, they should have developed adaptive strategies to cope with the very low oxygen levels characteristic of this habitat (Seibel, 2011).

In the rest of the ocean, the predicted DVM depths are in reasonable agreement with the acoustic Doppler current profiler observations. Migration depths tend to be deeper in oligotrophic areas, close to 500 m, whereas they are less than 400 m in more productive regions such as the equatorial regions and the middle and high latitudes of the Northern Hemisphere. In the Southern Ocean, the few available observations show rather deep migrations, in general deeper than 500 m, similar to what is observed in the oligotrophic subtropical gyres. Our model fails to predict these deep migration depths, which suggest other control cues than only the light preferendum as hypothesized in NPA. Part of this bias might also be explained by the too elevated chlorophyll concentrations predicted in this region that result in a too strong vertical attenuation of light. Nevertheless, despite the significant biases in the Southern Ocean and over the anoxic areas, NPA performs reasonably well at predicting migration depths over most of the global ocean. Thus, this tends to confirm the light preferendum hypothesis, which proves to be a valid simple mechanistic assumption for modeling DVMs at the global scale. A similar conclusion has been achieved by Aksnes et al. (2017) based on a large scale acoustic sampling.

Evaluation of the predicted migratory biomass is challenging because of the rather limited number of observations available in the literature. Only 96 observations have been collected from a survey of the literature, a small number also explained by the difficulty to extract the data from the published studies (see section 2.3). In an attempt to increase the number of observations, the COPEPOD database has been analyzed to extract the migratory biomass from the difference between daytime and nighttime in situ observations of biomass. Figure 4 presents a statistical analysis of the contribution of migrating organisms to the total epipelagic community. This analysis is applied in the model to mesozooplankton and macrozooplankton, which are the size

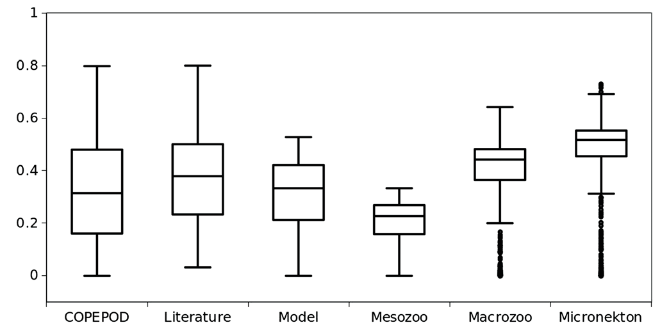

Figure 4. Box-whisker plot of the contribution of migratory organisms to the total epipelagic biomass. Coastal and Oceanic Plankton Ecology, Production, and Observation Database (COPEPOD) and Literature correspond to the statistical analysis performed with, respectively, the COPEPOD-2014 database and our survey of the literature (see section 2.3 for more information). Model corresponds to the model results sampled at the exact location of the COPEPOD data. In Model, the analysis is restricted to mesozooplankton and macrozooplankton (between 0.2 and 2 cm). Mesozoo, Macrozoo, and micronekton display the statistical analysis performed on the corresponding size classes simulated by PISCES-APECOSM defined as 0.2–2 mm, 0.2–2 cm, and 2–20 cm, respectively.

classes sampled in the COPEPOD database. We have restricted the analysis to a globally averaged statistical characterization of the data because observations do not show any coherent visible large-scale spatial patterns (not shown). The median of the modeled relative biomass of migratory organisms is close to that computed from the observations, 0.33 and 0.32, respectively. The mean contributions are close to the median values both in the model and in the observations: On average, 30% of the upper ocean biomass is performing diel vertical migration in the model and 33% in the observations. The observed contribution is significantly more variable with a standard deviation of 0.21, whereas the modeled standard deviation equals 0.15. In particular, the model does not display high contributions above 50%, whereas migratory relative biomass can exceed 80% in the data. A similar statistical analysis has been performed on the data that have been collected from our survey of the literature. The mean and median are both equal to 0.38 and are thus higher than the values computed from both the COPEPOD database and the model outputs.

Figure 4 also displays statistics for different size fractions, that is, mesozooplankton (0.2–2 mm), macrozooplankton (2 mm to 2 cm), and micronekton (2–20 cm). Mesozooplankton is predicted to have the smallest relative migratory biomass with a mean and median which are both close to 0.23. In the model, only organisms larger than 1 mm are assumed to be able to perform marked DVM. This is partly consistent with the observations that show that only a small fraction of the smallest mesozooplankton size classes migrates and their migration often remains confined within the upper ocean (e.g., Head et al., 1999; Madin et al., 2001; Rodier & Le Borgne, 1997). The fractional migratory biomass is predicted to increase with the size of the organisms, such that micronekton has both the largest mean and median values, respectively 0.46 and 0.52. However, even for the largest size classes, the model is not able to predict the high fractional biomass that have been observed.

The annual-mean spatial distribution of the relative migratory biomass simulated by the model is shown in Figure 5. Observations obtained from our survey of the literature are also shown in that figure. The modeled distribution exhibits only modest spatial variations. As evidenced in our statistical analysis, the model is not able to predict the high migratory contributions that can exceed 70% in some observations. In the tropical regions, the contribution is relatively homogeneous with values close to 45% except in areas characterized by intense shallow anoxic zones such as in the Arabian Sea and the eastern equatorial Pacific Ocean. In the high latitudes of both hemispheres, contributions tend to be lower, below 30%. The limited number of observations is not sufficient to perform a robust evaluation of the model behavior. However, as in the model, the in situ data do not suggest strong spatial variations with most values ranging between 30% and 50%. The lowest values found in the observations (e.g., in the central equatorial Pacific) correspond to measurements restricted to mesozooplankton for which only the largest organisms (larger than 1 mm) perform marked vertical migrations (e.g., Le Borgne et al., 2003; Rodier & Le Borgne, 1997).

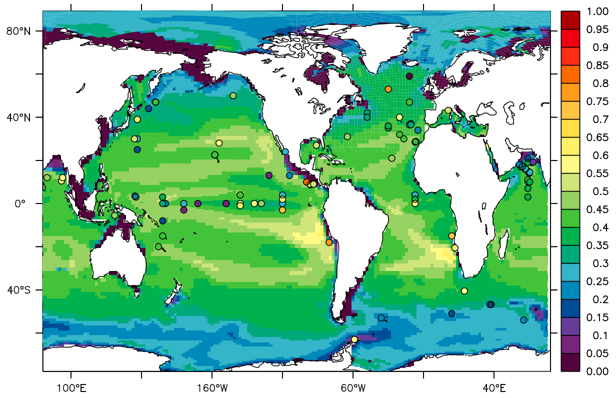

Figure 5. Contribution of the migratory organisms to the total epipelagic biomass. The epipelagic domain is considered to be the top 150 m of the ocean. Only mesozooplankton and macrozooplankton are included in the analysis. Colored circles display available observations collected from the literature (see section 2.3 for more information).

3.3. Predicted Active Flux of Carbon

The annual-mean spatial distribution of active flux induced by migrating organisms is represented in Figure 6a. The analysis is restricted here to mesozooplankton and macrozooplankton as almost no estimates in our survey of the literature include larger organisms such as fishes and large crustaceans (but see, e.g., Davison et al., 2013; Schukat et al., 2013). Maximum export (10–30 mg C$\cdot$m$^{-2}\cdot$day^{-1}) is simulated in the equatorial regions, off the eastern boundary upwelling systems. In the midlatitudes of both hemispheres, around 30° to 45°, active export is also elevated with maximum values in the western part of the ocean basins. In the oligotrophic subtropical gyres, rates are modest (1–4 mg C$\cdot$m$^{-2}\cdot$day^{-1}). Active fluxes of C are minimum in the polar regions, with rates lower than

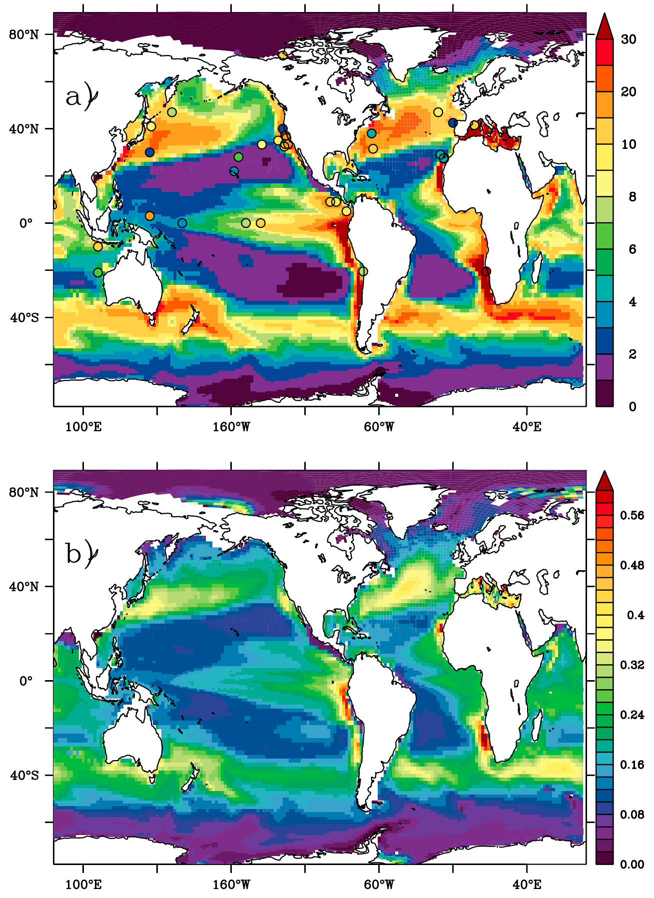

Figure 6. Active transport of carbon induced by DVM at 150 m. (a) Annual-mean export of carbon due to this active transport (in mg C$\cdot$m$^{-2}\cdot$day^{-1}). (b) Annual-mean ratio of the active transport of carbon over the export driven by sinking particles at 150 m. Colored circles on panel (a) display available observations (see section 2.3 for more information).

2 mg C$\cdot$m$^{-2}\cdot$day^{-1}. Fluxes generally exhibit local minima in regions with anoxic waters in the subsurface, such as the eastern Pacific Ocean and the Arabian Sea. The simulated DVM depths in these regions are very shallow because the habitat is constrained by the lack of oxygen (Figure 3). As a consequence, migrating organisms remain above the 150-m horizon defined here to compute the carbon export. Overall, the large scale spatial patterns of active fluxes of C share some similarities with the passive export of carbon, with the notable exception of the very low values in the polar regions and over anoxic areas (Henson et al., 2012; Laws et al., 2000).

Assessing the simulated active export of C is rather challenging due to the scarcity of observations. Figure 6a also shows the data points that we have been able to collect from the literature. The predicted active fluxes of carbon are of the right order of magnitude as indicated by the observations. Proper assessment of the spatial patterns is not feasible. Nevertheless, observations show significant active export in the northern subtropical gyre of the Pacific in contrast with the model prediction. This suggests that the model might underestimates the active transport of carbon in the oligotrophic subtropical gyres. The very low simulated rates in the polar regions cannot be assessed due to the lack of data, even if one study performed near the Antarctic Peninsula found very low active export (Yebra et al., 2009). On the other hand, high active transport rates have been observed in one study achieved in the Arctic Ocean (Darnis & Fortier, 2012).

The ratio of active transport of carbon to the passive export by sinking particles is shown in Figure 6b. The distribution shares some similarities with the spatial patterns of the active fluxes. High ratios, about 0.3 to 0.4, are simulated in the tropical regions and at midlatitudes. The highest values, above 0.5, are reached offshore the eastern boundary upwelling systems. The oligotrophic subtropical gyres are characterized by modest values (0.1–0.2). Minimum ratios (< 0.1) are produced in the polar regions and also in regions characterized by intense OMZs. Ratios are high in eastern boundary upwelling systems such as off California and off western Africa. This result seems in contradiction with the study by Davison et al. (2013). In their study focused on mesopelagic fishes in the California Current ecosystem and in the North Pacific subtropical gyre, they found minimum ratios close to the coast increasing offshore toward the more oligotrophic waters of the subtropical gyre. A potential explanation to that discrepancy may be the constant metabolism that has been assumed in that study, which is thus identical in productive and nonproductive systems. In our model, a large fraction of the metabolism is made a function of the grazing intensity and then of the prey abundance.

Table 3
Annual Global Export of Carbon at 150 m (Pg C/year)

Fluxes	Total `NoMig`	Total `Std`	Mesozooplankton (0.2–2 mm)	Macrozooplankton (0.2–2 cm)	Fishes (> 2 cm)
NPP	42.9	37.7 ± 2.4			
Passive export	6.5	5.7 ± 0.1			
Active export		1.05 ± 0.15	0.43	0.43	0.19
Respiration		0.52 ± 0.08	0.20	0.21	0.11
Egestion		0.37 ± 0.05	0.15	0.16	0.06
Predation		0.16 ± 0.02	0.08	0.06	0.02

Note. In the second column, the standard deviations are computed from the sensitivity experiments detailed in section 4.2. Predation also includes natural mortality.

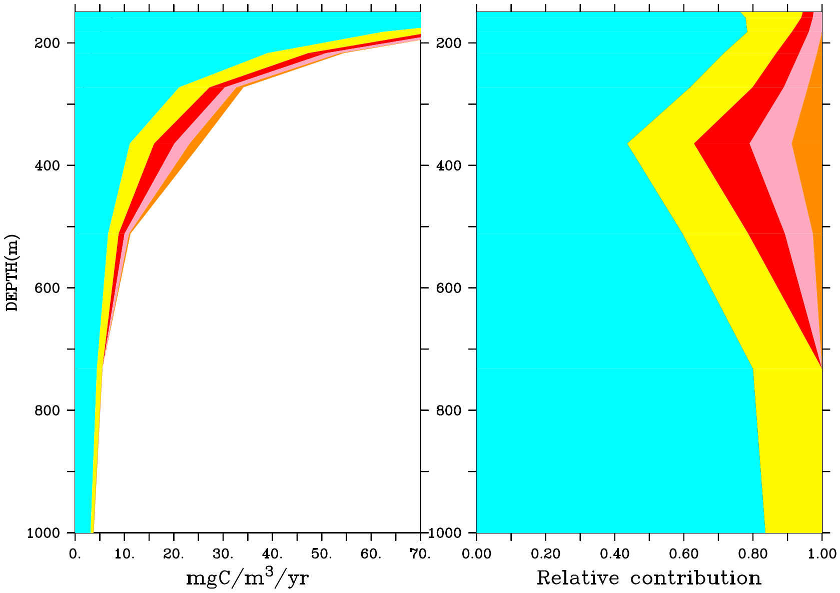

Figure 7. Annual-mean cumulated fluxes of carbon (left panel, in mg C·m^{-3}·year^{-1}) in the mesopelagic domain and their annual-mean relative contribution (right panel). The blue shaded area corresponds to bacterial degradation of sinking particles and dissolved organic matter. The yellow shaded area shows respiration by nonmigrating marine organisms. The red shaded area displays respiration by migrating organisms. The pink shaded area is the detritus production by migrating organisms, and the orange shaded area corresponds to grazing of migrating organisms by nonmigrating organisms. Fluxes have been averaged over the global ocean.

Table 3 shows the global fluxes of carbon in our standard simulation. The passive flux of carbon equals 5.7 Pg C/year, which lies within the range of published estimates (Henson et al., 2011; Laws et al., 2000; Lutz et al., 2007; Siegel et al., 2014). The global active export of carbon is 1.05 Pg C/year and thus represents 18% of the global passive export of carbon from the upper ocean (the passive transport of DOC by ocean currents and mixing is omitted here despite that it can represent a significant fraction of the total export). We are not aware of any previously published global estimates of this export. In situ studies have found contributions that range from less than 5% to more than 70% (e.g., Darnis & Fortier, 2012; Kobari et al., 2013; Yebra et al., 2009). Respiration by migrating organisms represents the dominant process (50%). Egestion of fecal pellets accounts for 35%, whereas natural mortality and grazing of migratory organisms by the mesopelagic community are smaller, yet significant (15%). A large proportion of the active flux is caused by mesozooplankton and macrozooplankton, which are predicted to drive a quite similar proportion of this flux. Larger organisms such as fishes and large crustaceans are predicted to induce a smaller flux of 0.19 Pg C/year, that is, 18% of the total active flux. The contribution of these large organisms never exceeds 25% in the model which seems to be in contradiction with in situ observations which have found much higher contributions (Davison et al., 2013; Schukat et al., 2013).

Most of the carbon that is exported below the upper ocean is ultimately respired in the mesopelagic domain above 1,000 m. However, the vertical distribution of this carbon flux varies greatly with the process considered (Figure 7). The dominant process at all depth is remineralization of particles sinking from the upper ocean. Respiration by nonmigrating marine organisms is also a significant process which represents about 20% of the total release of carbon. The magnitude of both processes decreases strongly with depth, especially in the upper mesopelagic domain. Between about 200 and 600 m, fluxes driven by migratory organisms (respiration, egestion, natural mortality, and grazing of migrating organisms by nonmigratory mesopelagic organisms) become major sources of carbon with a maximum contribution of 37% at about 350 m. Migrating organisms could thus sustain a significant fraction of the C demand in the mesopelagic domain (Burd et al., 2010; Steinberg, Van Mooy, e tal., 2008).

4. Discussion

4.1. Model Caveats

The model study presented here is based on a highly idealized description of marine ecosystems. Since our study focuses on DVM, we will only discuss here the assumptions that have been made to parameterize DVM in the model. The depth at which the organisms migrate has been hypothesized to be mainly controlled by the light level, except when oxygen levels are not sufficient to sustain respiration. This assumption is based on the light preferendum hypothesis, which has received considerable attention in the literature (e.g., Cohen & Forward, 2009; Frank & Widder, 2002). However, alternative explanations have been proposed. In particular, Bianchi, Galbraith, et al. (2013) have shown that the oxygen gradient between the upper ocean and the mesopelagic zone is a better predictor of DVM amplitude than light levels. Migrating organisms swim to low-oxygen zones to escape predation from large predators requiring higher levels of oxygen as a consequence of their strong swimming activity and of their large size (Seibel, 2011; Stramma et al., 2012). In the areas with no OMZ, migrators have to swim deeper in the water column to escape visual predation light levels control the amplitude of the DVM. According to this hypothesis, oxygen would be the primary cue and light level would be the secondary cue, whereas we supposed in our model a simultaneous colimitation. In fact, both hypotheses produce rather similar spatial patterns of DVM depths (see Figure 3). As already discussed, the largest differences occur in areas characterized by very strong anoxic subsurface waters. However, this is directly linked to the minimum oxygen threshold chosen in our model. Assuming a lower threshold would have produced a better agreement in those regions (not shown). This suggests that our oxygen threshold is too restrictive. Nevertheless, even with a lower oxygen threshold, simulated DVM depths could not reach the core of anoxic zones. Yet observations show that some migrating organisms can cope with virtually null oxygen concentrations by adopting adaptive specific strategies (Bianchi et al., 2014; Seibel, 2011).

We assume in PISCES-APECOSM that all organisms swim to the same depth. In reality, DVM vertical patterns are often more complicated. Acoustic observations commonly highlight several migrating scattering layers (e.g., Cisewski et al., 2010; Heywood, 1996; Pinot & Jansá, 2001). Thus, in general, different plankton communities perform DVMs with different vertical amplitudes, timing and vertical swimming speeds. A potential explanation to these contrasted behaviors can be size. Small organisms tend to perform shallower migrations than larger organisms (De Robertis, 2002; Hays et al., 1994; Pinot & Jansá, 2001; Steinberg, Van Mooy, et al., 2008). For instance, copepods have a migration amplitude of typically 50 to 100 m, the larger stages migrating deeper than the smaller stages (Atkinson et al., 1996; Irigoien et al., 2004). This amplitude is much shallower than the DVM depths predicted by our model, which are more typical of euphausiids, salps, and myctophiids. Pigmentation can also explain some of the differences in the observed migration patterns. More pigmented organisms tend to perform larger migrations as they are more visible to visual predators (Bollens et al., 1993; Hays, 2003). The consequences of these simplifications in our model are difficult to evaluate. If the migrating organisms can fully escape predation when they are in their refuge habitat, the exact depth at which organisms reside should not make a difference on the benefit of migrating as a predator avoidance strategy. In the tropical regions, deeper migration would lead to lower temperature which would minimize more maintenance costs but at the expense of slower growth rates such that the net effect is rather complicated to anticipate (Enright, 1977; Loose & Dawidowicz, 1994; Pangle & Peacor, 2006). In terms of the efficiency of the carbon export driven by DVM, shallower migration depth should tend to decrease the long term sequestration of carbon. As a consequence, NPA might have overestimated the efficiency of DVM, at least for the smallest size classes.

Typical migrating organisms descend at depth during daytime and return to the surface at night to feed on the epipelagic community. However, reverse migration patterns are commonly observed in the ocean. This unusual behavior is commonly explained by a predator avoidance mechanism: Organisms undergo reverse migration patterns to escape their predators that perform regular migrations (Neill, 1990; Ohman et al., 1983). Since our model does not consider reverse migrations, it should overestimate predation within the migratory community. On the other hand, reverse migrators become available to visual predators since they move to the surface during daytime. Furthermore, in the middle and high latitudes where day and night durations differ markedly in summer and winter, reverse migrations alter the duration of the feeding period. They should also change the efficiency of DVM as a carbon pump, since it is directly proportional to the time organisms spend in the mesopelagic zone.

Several other processes involved in DVM have been omitted in our model. Migrators are assumed to rest when they descend to the mesopelagic zone. Yet some predators follow their preys and continue to feed on migratory organisms in deep waters. Furthermore, we made the assumption that the migratory community is distinct from the other modeled communities. In fact, many organisms might be able to change their behavior over time. The age, the sex, and the body condition may have an impact on DVM (Hays, Kennedy, et al., 2001; Miljeteig et al., 2014; Shea & Vecchione, 2010). In the high latitudes, some observations have found that DVM may stop during periods of midnight sun and polar night (Blachowiak-Samolyk et al., 2006; Falkenhaug et al., 1997; Fischer & Visbeck, 1993) although this remains controversial (Berge et al., 2009; Cottier et al., 2006). During wintertime, many species perform ontogenetic seasonal migrations and reside in the mesopelagic domain (Shimode et al., 2009; Yamaguchi et al., 2010). Thus, overlaps might exist in reality between the three modeled communities in contrast to what is assumed in the model.

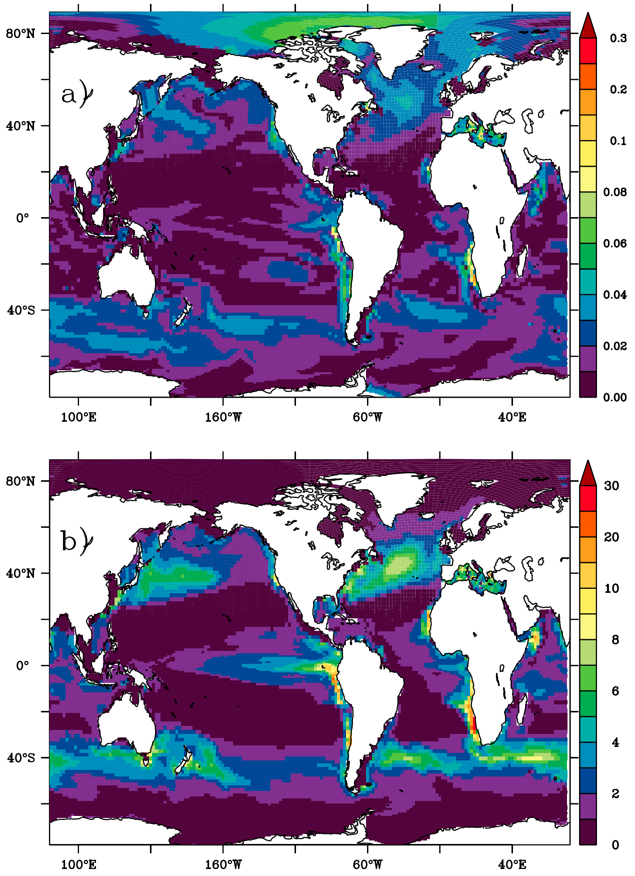

Figure 8. Annual-mean standard deviation of the contribution of migrating organisms to the total epipelagic biomass (a) and of the active transport of carbon driven by migrators (b). Active transport is in mg C·m^{-2}·day^{-1}. Standard deviation has been computed from the four sensitivity experiments in addition to the standard experiment.

4.2. Sensitivity to Parameters

The results presented in this study are of course sensitive to the choice of parameters. A complete sensitivity analysis of the model results would be extremely difficult to perform because both the biogeochemical model PISCES and the ecosystem model APECOSM include together more than 100 parameters. Since migrating organisms are modeled in APECOSM, we have restricted the analysis to some major parameters of the latter model. The half-saturation constant used in the functional response of predation and the ingestion rate have been varied by ±50% with respect to their standard values. Thus, a total of four sensitivity experiments have been performed and run for 20 years each, so that biomass and fluxes vary by less than 1% annually. Since maintenance rates are computed from ingestion rates in APECOSM, any variation in the ingestion rate translates to a similar variation of the maintenance rate (Maury et al., 2007). Furthermore, a unique set of parameters is used for the three modeled communities which means that any modification of these parameters affects not only the migrating community but also the epipelagic and mesopelagic communities.

Figure 8 shows the annual-mean standard deviations of the relative migrating biomass and of the active fluxes of carbon driven by DVM. Over most of the ocean, the relative contribution of migrators to the epipelagic biomass is rather insensitive to the variations of the parameters that were applied in the different sensitivity experiments. The standard deviation remains in general below 0.05. The largest changes are simulated in regions characterized by intense anoxic zones such as the eastern tropical Pacific Ocean and the Arabian Sea. In our sensitivity experiments, both the active and passive fluxes of carbon are modified and lead to changes in the depth of the oxycline. Since the oxycline, which strongly constrains the amplitude of DVM, is within the epipelagic domain (see Figure 3), its depth modulates the predation pressure by the epipelagic community when the organisms reside in their daytime habitat. A shallower oxycline produces a stronger grazing pressure, whereas a deeper oxycline alleviates this pressure and eventually, if it becomes deep enough, completely cancels it out. A relatively high standard deviation is also simulated in part of the Arctic Ocean whose explanation remains unclear.

The standard deviation of the active fluxes of carbon is more important than that of the relative contribution of the migrating organisms. Unsurprisingly, its spatial distribution is very similar to that of the active fluxes (see Figure 6). However, the relative changes in these fluxes remain lower than the variations applied to the parameters, generally below 30%. Larger metabolic rates increase the grazing pressure on the lower trophic levels which reduces the amount of energy available at the bottom of the trophic food web. As a consequence, the biomass of the three communities, including the migrating organisms, tends to decrease. This partly compensates for the higher metabolic rates.

In this study, we have designed a simple model of diel vertical migrations, in particular to assess their role in the biological carbon pump. This model is based on simplifying assumptions which prove to be questionable when confronted to observations. Furthermore, the set of parameters used in APECOSM (but also in PISCES)

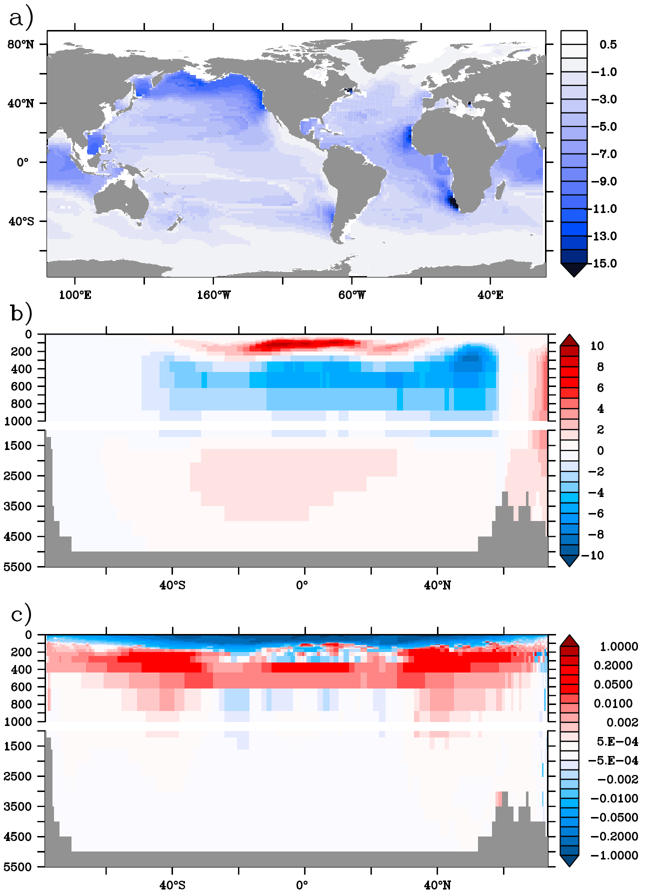

Figure 9. Simulated impact of diurnal vertical migration active transport on dissolved oxygen. (a) Annual-mean change in dissolved oxygen (μmol/L) averaged between 200 and 500 m. (b) Annual-mean change in oxygen zonally averaged over the global ocean (μmol/L). (c) Annual-mean change in respiration fluxes zonally averaged over the global ocean (mg C$\cdot$m$^{-3}\cdot$day^{-1}).

are highly uncertain with potentially important consequences on the simulated active fluxes of carbon. A major difficulty to modeling DVMs is the glaring lack of dedicated quantitative observations. Observations are indeed lacking in many regions of the ocean (Figure 5) and the seasonal evolution of DVM is almost never possible to investigate, at least with the data that we have been able to collect from our survey of the literature.

4.3. Impact of DVM on Oxygen

DVM has been the focus of many dedicated studies since its discovery a century ago (Murray & Hjort, 1912). The vast majority of these studies describes the characteristics of the vertical migrations in specific areas focusing very often on specific species or size classes. Acoustic surveys have improved our understanding of DVM by providing a detailed vertical description of the movements of sound scattering layers with an unrivaled temporal and spatial resolution. However, a quantitative understanding of DVM from both acoustic and traditional observations is rather challenging, especially when quantifying the active transport of carbon. As a consequence, only very few studies have estimated the flux of carbon driven by the diel vertical movements of marine organisms and almost all of them are based on local observations performed at a few stations (see section 2.3 for a list of these studies). The active transport of carbon has been estimated to range between 10% and 50% of the carbon exported by sinking particles. At global scale, we are aware of only two studies who have attempted to infer the biogeochemical impact of DVM. In a first study based on both observations and a global biogeochemical model, Bianchi, Galbraith, et al. (2013) have shown that migratory organisms intensify oxygen consumption in the mesopelagic domain, especially in the upper part of the OMZs. Overall, DVM is suggested to decrease oxygen concentrations on average by 15–46 mmol/m^3 between 150 and 500 m. This corresponds to the absolute change in oxygen that is driven by the active transport of carbon due to migrating organisms. In a second study based on a similar approach, Bianchi et al. (2014) suggested that excretion by migrating organisms can exceed the release of ammonium from sinking particles in anoxic areas and sustain significant rates of anammox. This could explain the decoupling between denitrification and anamox (Canfield et al., 2010; Lam et al., 2009).

The model used in the present study offers the opportunity to investigate the biogeochemical impact of DVM at the global scale within a fully integrated and consistent framework. In particular, diel vertical migrations are explicitly modeled in a fully prognostic mode and not prescribed as a fixed fraction of export production. The impacts of DVM on marine biogeochemistry has been inferred from the difference between the experiments `Std` and `NoMig`. This comparison may help revealing compensatory feedbacks between the direct impact of DVM on oxygen due to respiration and indirect impacts resulting from changes in primary production and in export efficiency to the ocean's interior. Figure 9 shows the net impact of DVM on oxygen as predicted by our model. As expected, respiration and egestion by migratory organisms induce a decrease in oxygen between 150 and 500 m, which reaches about 5 mmol/m^3 averaged globally at 500 m. Elevated oxygen anomalies are simulated in the subpolar North Pacific Ocean, whereas in the Arctic and Antarctic Oceans, the anomalies remain very small. Maximum oxygen anomalies are predicted in some of the eastern boundary upwelling systems where they can exceed 15 mmol/m^3. Such result is not surprising as this is where the active export of carbon is predicted to be the highest (Figure 6). In the eastern equatorial Pacific Ocean and in the Arabian Sea and the Bay of Bengal, oxygen anomalies are very small because anoxic waters occupy the vertical domain where oxygen differences have been averaged, such that oxygen levels cannot decrease much anyway. Furthermore, in those regions, the migration depth remains above or close to 150 m (Figure 3). Even above 150 m, differences remain modest (< 15 mmol O_2/m^3, not shown). Since migrations remain confined within the epipelagic domain, respiration during daytime consumes oxygen within the epipelagic ocean only, as it would in the absence of migration.

The vertical distribution of oxygen anomalies exhibits more complex patterns than just a decrease in the mesopelagic domain as evidenced in Figure 9a. Three distinct vertical layers can be distinguished. In the subsurface above 200 m, vertical migration generates a positive dissolved oxygen anomaly that can exceed 10 mmol O_2/m^3 when zonally averaged over the global ocean (Figure 9b). This anomaly is explained by a less intense respiration in the epipelagic domain due to the movement of the migrating organisms which instead respire deeper in the water column. As shown in Figure 6c, increased respiration is nevertheless sometimes predicted in the epipelagic domain of the tropical domain as a consequence of the presence of intense OMZs, which prevent migrating organisms to descend deeper in the water column (Figure 3). Further below, down to about 1,000 m, DVM produces a depletion in oxygen as a result of respiration by migrators that reside in the mesopelagic domain during daytime. Figure 9c underscores this increased oxygen consumption at the migration depth. In the middle and high latitudes, oxygen consumption is also increased below the migration depth because of the production of large particles in the mesopelagic domain by migrating organisms. Finally, in the bathypelagic domain (below 1,000 m), oxygen levels are increased by almost 2 mmol O_2/m^3 as a result of a slightly lower oxygen consumption. Such lower oxygen consumption in the deep ocean comes from a lower export by large particles produced in the euphotic zone (Table 3), which is not fully compensated for by the production of large particles at the migration depth, either by the migrating organisms or by the mesopelagic predators of the migrators. Such decreased oxygen consumption is also predicted between the migration depth and above 1,000 m in the low latitudes.

The oxygen anomalies driven by DVM remain relatively modest, even if they are significant. As proposed by Bianchi, Galbraith, et al. (2013), DVM intensify the oxygen depletion in the mesopelagic domain. However, due to compensating effects between respiration, egestion, and the trophic interactions due to the migrating organisms on one hand, and a lower export sustained by sinking particles on the other hand, oxygen levels are decreased significantly less than anticipated from the study by Bianchi, Galbraith, et al. (2013), who estimated the absolute oxygen deficit due to DVM. A direct quantitative comparison with this latter study would be unfortunately very difficult to perform. This would require to track in our model setup the oxygen consumption directly linked to the migrating community: respiration, the degradation of the fecal pellets produced by the migrating organisms when they reside in their deep habitat, and the oxygen consumption due to the mesopelagic community that grazes onto the migrating community and the particles that have been produced by the latter. The first process is easily accessible. The two other oxygen sinks are much more difficult to quantify because the model does not track the origin and fate of the organic matter in the different modeled living and nonliving pools. One could anticipate a significant oxygen consumption that would probably lead to a deficit with a magnitude roughly similar to what has been found by Bianchi, Galbraith, et al. (2013). Thus, even if at first sight, the impacts on oxygen may appear quantitatively very different between our study and that by Bianchi, Galbraith, et al. (2013), this difference is mainly explained by the fact that both studies diagnose different quantities. Bianchi, Galbraith, et al. (2013) investigate the imprint of DVM on oxygen whereas our study evaluates how oxygen distribution would differ in an ocean with or without DVM. From the results presented here, we conclude that due to compensatory effects, the distribution of oxygen is not strongly sensitive to DVM.

5. Conclusions

In this study, we investigated the diurnal vertical migration using a fully coupled model, which represents the entire pelagic ecosystem at the global scale. To our knowledge, this is the first time that such a global end-to-end ecosystem model is being used at the global scale as well as that DVM is explicitly modeled in a global ocean biogeochemical model. Assessing the model predictions has proved to be challenging because of the scarcity of suitable data that can be properly compared to the modeled fields. Nevertheless, the model appears to be able to simulate correctly the large-scale patterns of the migration depth, except in regions characterized by intense anoxia. In our model, marine organisms are not assumed to be able to cope with very low oxygen concentrations whereas observations suggest that some species would have developed specific adaptive strategies to descend in very anoxic waters. The simulated relative biomass of migratory organisms seems to be consistent, at least partly, with available observations. About one third of the epipelagic biomass (median relative contribution) is predicted to perform diurnal vertical migrations. The migratory relative biomass is on average higher in the low latitudes than in the high latitudes. It is also higher as the size of the organisms increases. Beyond these general patterns, in contrast with what some observations suggest, our model does not reproduce the very high migratory contributions that have sometimes been observed.

The global active flux of carbon is predicted to be 1.05 ± 0.15 Pg C/year, which represents 18% of the passive flux of carbon driven by sinking particles at 150 m. We are not aware of any published estimates of this active flux at the global scale that could be compared to our model. Comparison with local studies suggests that the model is able to capture the right order of magnitude of this flux, except perhaps in the oligotrophic subtropical gyres where it seems to be underestimated. Furthermore, micronekton and fishes contribute a relatively small fraction of the migratory flux of carbon, 18% on average and never more than 25%, whereas some studies have evidenced much higher contributions (Davison et al., 2013; Schukat et al., 2013). DVM has a significant impact on oxygen and on the sinking flux of particles to the interior of the ocean. Oxygen is decreased in the mesopelagic ocean in agreement with the study by Bianchi, Galbraith, et al. (2013). This decrease remains rather modest close to 5 mmol O_2/m^3. Thus, when DVM and its impacts on ocean biogeochemistry are fully modeled, intensification of oxygen depletion is significant but not very strong.

Despite its numerous uncertainties, our study concludes that DVM drive a significant flux of carbon to the interior of the ocean, similar in magnitude to the transport of DOC (Hansell et al., 2009; Najjar et al., 2007). The consequences of this flux on ocean biogeochemistry seem to be rather modest in our study, yet significant. There is thus an urgent need to better constrain this flux. Yet observations remain scarce and the processes that control DVM are still far from being fully understood. Future progress that will allow to better quantify the role of DVM for ocean biogeochemistry and for ecosystems dynamics will need a strong effort that could bring additional observational and experimental information. Only that effort will offer the possibility to build more robust models of DVM that can be ultimately embedded in ocean biogeochemical and climate models.

Acknowledgments
We thank everybody who participated to the development of the NPA model configuration. In particular, we especially thank Thomas Arsouze, Christian Ethé, Thomas Gorgues, Prune Strozzi, Laurent Mémery, and all the MACROES community whose help was invaluable, either by the technical developments and advice they contributed to and/or by the scientific discussions they stimulated. This study was funded by the ANR-MACROES and ANR-CIGOEF projects. Graphics have been produced with ferret. The code, the model outputs, and the COPEPOD-analyzed data that have been used in this study can be freely obtained from https://zenodo.org/record/1148151. They are referenced as Aumont Olivier, Maury Olivier, Bopp Laurent, and Lefort Stelly, Data set and code of NEMO-PISCES-APECOSM (version 1), Zenodo, http://doi.org/10.5281/zenodo.1148151, 2018.

References

Aksnes, D. L., & Giske, J. (1990). Habitat profitability in pelagic environments. *Marine Ecology Progress Series*, *64*, 209–215.

Aksnes, D. L., Røstad, A., Kaartvedt, S., Martinez, U., Duarte, C. M., & Irigoien, X. (2017). Light penetration structures the deep acoustic scattering layers in the global ocean. *Science Advances*, *5*, E1602468. https://doi.org/10.1126/sciadv.1602468

Al-Mutairi, H., & Landry, M. R. (2001). Active export of carbon and nitrogen at Station ALOHA by diel migrant zooplankton. *Deep Sea Research Part II: Topical Studies in Oceanography*, *48*(8), 2083–2103. https://doi.org/10.1016/S0967-0645(00)00174-0

Allison, S. K., & Wishner, K. F. (1986). Spatial and temporal patterns of zooplankton biomass across the Gulf Stream. *Marine Ecology Progress Series*, *31*(3), 233–243.

Anderson, K. P., & Ursin, E. (1977). The partitioning of natural mortality in a multispecies model of fishing and predation. In J. H. Steele (Ed.), *Fisheries Mathematics* (pp. 87–97). London, New York, San Francisco: Academic Press.

Atkinson, A., Ward, P., & Murphy, E. J. (1996). Diel periodicity of Subantarctic copepods: Relationships between vertical migration, gut fullness and gut evacuation rate. *Journal of Plankton Research*, *18*(8), 1387–1405. https://doi.org/10.1093/plankt/18.8.1387

Aumont, O., Ethé, C., Tagliabue, A., Bopp, L., & Gehlen, M. (2015). PISCES-v2: An ocean biogeochemical model for carbon and ecosystem studies. *Geoscientific Model Development Discussions*, *8*(2), 1375–1509.

Banse, K. (1964). On the vertical distribution of zooplankton in the sea. *Progress in Oceanography*, *2*, 55–125.

Barange, M. (1994). Acoustic identification, classification and structure of biological patchiness on the edge of the Agulhas Bank and its relation to frontal features. *South African Journal of Marine Science*, *14*(1), 333–347. https://doi.org/10.2989/025776194784286969

Barnier, B., Madec, G., Penduff, T., Molines, J.-M., Tréguier, A.-M., le Sommer, J., et al. (2006). Impact of partial steps and momentum advection schemes in a global ocean circulation model at eddy-permitting resolution. *Ocean Dynamics*, *56*, 543–567. https://doi.org/10.1007/s10236-006-0082-1

Berge, J., Båtnes, A. S., Johnsen, G., Blackwell, S. M., & Moline, M. A. (2012). Bioluminescence in the high Arctic during the polar night. *Marine Biology*, *159*(1), 231–237. https://doi.org/10.1007/s00227-011-1798-0

Berge, J., Cottier, F., Last, K. S., Varpe, O., Leu, E., Søreide, J., et al. (2009). Diel vertical migration of Arctic zooplankton during the polar night. *Biology Letters*, *5*(1), 69–72. https://doi.org/10.1098/rsbl.2008.0484

Bianchi, D., Babbin, A. R., & Galbraith, E. D. (2014). Enhancement of anammox by the excretion of diel vertical migrators. *Proceedings of the National Academy of Sciences*, *111*(44), 15,653–15,658. https://doi.org/10.1073/pnas.1410790111

Bianchi, D., Galbraith, E. D., Carozza, D. A., Mislan, K. A. S., & Stock, C. A. (2013). Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nature Geoscience*, *6*(7), 545–548. https://doi.org/10.1038/ngeo1837

Bianchi, D., & Mislan, K. A. S. (2016). Global patterns of diel vertical migration times and velocities from acoustic data. *Limnology and Oceanography*, *61*(1), 353–364. https://doi.org/10.1002/lno.10219

Bianchi, D., Stock, C., Galbraith, E. D., & Sarmiento, J. L. (2013). Diel vertical migration: Ecological controls and impacts on the biological pump in a one-dimensional ocean model. *Global Biogeochemical Cycles*, *27*, 478–491. https://doi.org/10.1002/gbc.20031

Blachowiak-Samolyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., et al. (2006). Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Marine Ecology Progress Series*, *308*, 101–116.

Blanke, B., & Delecluse, P. (1993). Low frequency variability of the tropical Atlantic Ocean simulated by a general circulation model with mixed layer physics. *Journal of Physical Oceanography*, *23*, 1363–1388.

Bollens, S. M., Frost, B. W., & Cordell, J. R. (1995). Diversity of cues in zooplankton vertical migration—A reply to Ringelberg's comment. *Journal of Plankton Research*, *17*(3), 656–658. https://doi.org/10.1093/plankt/17.3.656

Bollens, S. M., Osgood, K., Frost, B. W., & Watts, S. D. (1993). Vertical distributions and susceptibilities to vertebrate predation of the marine copepods Metridia lucens and Calanus pacificus. *Limnology and Oceanography*, *38*(8), 1827–1837. https://doi.org/10.4319/lo.1993.38.8.1827

Buesseler, K. O., & Boyd, P. W. (2009). Shedding light on processes that control particle export and flux attenuation in the twilight zone of the open ocean. *Limnology and Oceanography*, *54*, 1210–1232.

Buitenhuis, E. T., Vogt, M., Moriarty, R., Bednarsek, N., Doney, S. C., Leblanc, K., et al. (2013). MAREDAT: Towards a world atlas of MARine Ecosystem DATa. *Earth System Science Data*, *5*(2), 227–239.

Burd, A. B., Hansell, D. A., Steinberg, D. K., Anderson, T. R., Arístegui, J., Baltar, F., et al. (2010). Assessing the apparent imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: What the fuck is wrong with present calculations of carbon budgets? *Deep Sea Research Part II: Topical Studies in Oceanography*, *57*(16), 1557–1571. https://doi.org/10.1016/j.dsr2.2010.02.022

Canfield, D. E., Stewart, F. J., Thamdrup, B., Brabandere, L. D., Dalsgaard, T., Delong, E. F., et al. (2010). A cryptic sulfur cycle in oxygen-minimum-zone waters off the Chilean Coast. *Science*, *330*(6009), 1375–1378. https://doi.org/10.1126/science.1196889

Champalbert, G., Neveux, J., Gaudy, R., & Le Borgne, R. (2003). Diel variations of copepod feeding and grazing impact in the high-nutrient, low-chlorophyll zone of the equatorial Pacific Ocean (0°; 3°S, 180°). *Journal of Geophysical Research*, *108*(C12), 8145. https://doi.org/10.1029/2001JC000810

Champalbert, G., Pagano, M., Kouamé, B., & Riandey, V. (2005). Zooplankton spatial and temporal distribution in a tropical oceanic area off West Africa. *Hydrobiologia*, *548*(1), 251–265. https://doi.org/10.1007/s10750-005-5194-y

Cisewski, B., Strass, V. H., Rhein, M., & Krägefsky, S. (2010). Seasonal variation of diel vertical migration of zooplankton from ADCP backscatter time series data in the Lazarev Sea, Antarctica. *Deep Sea Research Part I: Oceanographic Research Papers*, *57*(1), 78–94.

Cohen, J. H., & Forward, R. B. (2009). Zooplankton diel vertical migration — A review of proximate control. *Oceanography and Marine Biology: An Annual Review*, *47*, 77–110.

Cook, A. B., Sutton, T. T., Galbraith, J. K., & Vecchione, M. (2013). Deep-pelagic (0-3000m) fish assemblage structure over the Mid-Atlantic Ridge in the area of the Charlie-Gibbs Fracture Zone. *Deep Sea Research Part II: Topical Studies in Oceanography*, *98*, 279–291. https://doi.org/10.1016/j.dsr2.2012.09.003

Cottier, F. R., Tarling, G. A., Wold, A., & Falk-Petersen, S. (2006). Unsynchronised and synchronised vertical migration of zooplankton in a high Arctic fjord. *Limnology and Oceanography*, *51*(6), 2586–2599. https://doi.org/10.4319/lo.2006.51.6.2586

Courant, R., Friedrichs, K., & Lewy, H. (1928). über die partiellen differenzengleichungen der mathematischen physics. *Mathematische Annalen*, *100*, 32–74.

Dam, H. G., Miller, C. A., & Jonasdottir, S. H. (1993). The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic Bloom Experiment. *Deep Sea Research Part II: Topical Studies in Oceanography*, *40*(1), 197–212. https://doi.org/10.1016/0967-0645(93)90013-D

Dam, H. G., Roman, M. R., & Youngbluth, M. J. (1995). Downward export of respiratory carbon and dissolved inorganic nitrogen by diel-migrant mesozooplankton at the JGOFS Bermuda time-series station. *Deep Sea Research Part I: Oceanographic Research Papers*, *42*(7), 1187–1197. https://doi.org/10.1016/0967-0637(95)00048-B

Darnis, G., & Fortier, L. (2012). Zooplankton respiration and the export of carbon at depth in the Amundsen Gulf (Arctic Ocean). *Journal of Geophysical Research*, *117*, C04013. https://doi.org/10.1029/2011JC007374

Datta, S., Delius, G. W., Law, R., & Plank, M. J. (2011). A stability analysis of the power-law steady state of marine size spectra. *Journal of Mathematical Biology*, *63*(4), 779–799. https://doi.org/10.1007/s00285-010-0387-z

Davison, P. C., Checkley, D. M. Jr., Koslow, J. A., & Barlow, J. (2013). Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Progress in Oceanography*, *116*, 14–30. https://doi.org/10.1016/j.pocean.2013.05.013

Dawidowicz, P., & Loose, C. J. (1992). Metabolic costs during predator-induced dielvertical migration of Daphnia. *Limnology and Oceanography*, *37*(8), 1589–1595. https://doi.org/10.4319/lo.1992.37.8.1589

De Robertis, A. (2002). Size-dependent visual predation risk and the timing of vertical migration: An optimization model. *Limnology and Oceanography*, *47*(4), 925–933.

Décima, M., Landry, M. R., & Rykaczewski, R. R. (2011). Broad scale patterns in mesozooplankton biomass and grazing in the eastern equatorial Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography*, *58*(3), 387–399. https://doi.org/10.1016/j.dsr2.2010.08.006

Décima, M., Landry, M. R., Stukel, M. R., Lopez-Lopez, L., & Krause, J. W. (2016). Mesozooplankton biomass and grazing in the Costa Rica Dome: Amplifying variability through the plankton food web. *Journal of Plankton Research*, *38*(2), 317–330. https://doi.org/10.1093/plankt/fbv091

Dietze, H., & Loeptien, U. (2013). Revisiting “nutrient trapping” in global coupled biogeochemical ocean circulation models. *Global Biogeochemical Cycles*, *27*, 265–284. https://doi.org/10.1002/gbc.20029

Duteil, O., Schwarzkopf, F. U., Böning, C. W., & Oschlies, A. (2014). Major role of the equatorial current system in setting oxygen levels in the eastern tropical Atlantic Ocean: A high-resolution model study. *Geophysical Research Letters*, *41*, 2033–2040. https://doi.org/10.1002/2013GL058888

Ekau, W., Auel, H., Pörtner, H.-O., & Gilbert, D. (2010). Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences*, *7*(5), 1669–1699.

Emerson, S., Quay, P., Karl, D., Winn, C., Tupas, L., & Landry, M. (1997). Experimental determination of the organic carbon flux from open-ocean surface waters. *Nature*, *389*(6654), 951–954. https://doi.org/10.1038/40111

Enright, J. T. (1977). Diurnal vertical migration: Adaptive significance and timing. Part 1. Selective advantage: A metabolic model1. *Limnology and Oceanography*, *22*(5), 856–872. https://doi.org/10.4319/lo.1977.22.5.0856

Escribano, R., Hidalgo, P., & Krautz, C. (2009). Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000. *Deep Sea Research Part II: Topical Studies in Oceanography*, *56*(16), 1083–1094. https://doi.org/10.1016/j.dsr2.2008.09.009

Falkenhaug, T., Tande, K. S., & Semenova, T. (1997). Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. *Marine Ecology Progress Series*, *149*(1/3), 105–119.

Falkowski, P. G., Laws, E. A., Barber, R. T., & Murray, J. W. (2003). Phytoplankton and their role in primary, new, and export production. In M. J. R. Fasham (Ed.), *Ocean Biogeochemistry* (pp. 99–121), Global Change – The IGBP Series (closed). Heidelberg: Springer Berlin. https://doi.org/10.1007/978-3-642-55844-3

Faugeras, B., & Maury, O. (2007). Modeling fish population movements: From an individual-based representation to an advection-diffusion equation. *Journal of Theoretical Biology*, *247*(4), 837–848. https://doi.org/10.1016/j.jtbi.2007.04.012

Fernández-Urruzola, I., Osma, N., Gómez, M., Pollehne, F., Postel, L., & Packard, T. T. (2016). Modeling downward particulate organic nitrogen flux from zooplankton ammonium regeneration in the northern Benguela. *Progress in Oceanography*, *149*, 121–133.

Fiksen, O., & Carlotti, F. (1998). A model of optimal life history and diel vertical migration in Calanus finmarchicus. *Sarsia*, *83*(2), 129–147. https://doi.org/10.1080/00364827.1998.10413678

Fischer, J., & Visbeck, M. (1993). Seasonal variation of the daily zooplankton migration in the Greenland sea. *Deep Sea Research Part I: Oceanographic Research Papers*, *40*(8), 1547–1557. https://doi.org/10.1016/0967-0637(93)90015-U

Frank, T., & Widder, E. (2002). Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton. *Marine Biology*, *140*(6), 1181–1193. https://doi.org/10.1007/s00227-002-0788-7

Fulton, E. A. (2010). Approaches to end-to-end ecosystem models. *Journal of Marine Systems*, *81*(1–2), 171–183. https://doi.org/10.1016/j.jmarsys.2009.12.012

Gabriel, W., & Thomas, B. (1988). Ultimate causes of vertical migration in zooplankton: An evaluation by evolutionary game theory, *Ecodynamics* pp. 127–134). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-73953-8

Garcia, C. A. E., Garcia, V. M. T., & McClain, C. R. (2005). Evaluation of SeaWiFs chlorophyll algorithms in the southwestern Atlantic and Southern Oceans. *Remote Sensing of Environment*, *95*(1), 125–137.

Gent, P. R., & McWilliams, J. C. (1990). Isopycnal mixing in ocean circulation models. *Journal of Physical Oceanography*, *20*, 150–155.

Guidi, L., Jackson, G. A., Stemmann, L., Miquel, J. C., Picheral, M., & Gorsky, G. (2008). Relationship between particle size distribution and flux in the mesopelagic zone. *Deep Sea Research Part I: Oceanographic Research Papers*, *55*(10), 1364–1374. https://doi.org/10.1016/j.dsr.2008.05.014

Hansell, D. A., & Carlson, C. A. (2001). Biogeochemistry of total organic carbon and nitrogen in the Sargasso Sea: Control by convective overturn. *Deep Sea Research Part II: Topical Studies in Oceanography*, *48*(8–9), 1649–1667. https://doi.org/10.1016/S0967-0645(00)00153-3

Hansell, D. A., Carlson, C. A., Repeta, D. J., & Schlitzer, R. (2009). Dissolved organic matter in the ocean a controversy stimulates new insights. *Oceanography*, *22*(SPL.ISS. 4), 202–211. https://doi.org/10.5670/oceanog.2009.109

Hartvig, M., Andersen, K. H., & Beyer, J. E. (2011). Food web framework for size-structured populations. *Journal of Theoretical Biology*, *272*(1), 113–122. https://doi.org/10.1016/j.jtbi.2010.12.006

Haury, L., Fey, C., Newland, C., & Genin, A. (2000). Zooplankton distribution around four eastern North Pacific seamounts. *Progress in Oceanography*, *45*(1), 69–105. https://doi.org/10.1016/S0079-6611(99)00051-8

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations, *Migrations and Dispersal of Marine Organisms* (pp. 163–170). Dordrecht: Springer.

Hays, G. C., Harris, R. P., & Head, R. N. (2001). Diel changes in the near-surface biomass of zooplankton and the carbon content of vertical migrants. *Deep Sea Research Part II: Topical Studies in Oceanography*, *48*(4), 1063–1068. https://doi.org/10.1016/S0967-0645(00)00109-0

Hays, G. C., Kennedy, H., & Frost, B. W. (2001). Individual variability in diel vertical migration of a marine copepod: Why some individuals remain at depth when others migrate. *Limnology and Oceanography*, *46*(8), 2050–2054. https://doi.org/10.4319/lo.2001.46.8.2050

Hays, G. C., Proctor, C. A., John, A. W. G., & Warner, A. J. (1994). Interspecific differences in the diel vertical migration of marine copepods: The implications of size, color, and morphology. *Limnology and Oceanography*, *39*(7), 1621–1629. https://doi.org/10.4319/lo.1994.39.7.1621

Head, R. N., Harris, R. P., Bonnet, D., & Irigoien, X. (1999). A comparative study of size-fractionated mesozooplankton biomass and grazing in the North East Atlantic. *Journal of Plankton Research*, *21*(12), 2285–2308. https://doi.org/10.1093/plankt/21.12.2285

Henson, S. A., Sanders, R., & Madsen, E. (2012). Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. *Global Biogeochemical Cycles*, *26*, GB1028. https://doi.org/10.1029/2011GB004099

Henson, S. A., Sanders, R., Madsen, E., Morris, P. J., Le Moigne, F., & Quartly, G. D. (2011). A reduced estimate of the strength of the ocean's biological carbon pump. *Geophysical Research Letters*, *38*, L04606. https://doi.org/10.1029/2011GL046735

Hernández-León, S., Gómez, M., Pagazaurtundua, M., Portillo-Hahnefeld, A., Montero, I., & Almeida, C. (2001). Vertical distribution of zooplankton in Canary Island waters: Implications for export flux. *Deep Sea Research Part I: Oceanographic Research Papers*, *48*(4), 1071–1092. https://doi.org/10.1016/S0967-0637(00)00074-1

Heywood, K. J. (1996). Diel vertical migration of zooplankton in the Northeast Atlantic. *Journal of Plankton Research*, *18*(2), 163–184. https://doi.org/10.1093/plankt/18.2.163

Hidaka, K., Kawaguchi, K., Murakami, M., & Takahashi, M. (2001). Downward transport of organic carbon by diel migratory micronekton in the western equatorial Pacific:. *Deep Sea Research Part I: Oceanographic Research Papers*, *48*(8), 1923–1939. https://doi.org/10.1016/S0967-0637(01)00003-6

Hood, R. R., Kohler, K. E., McCreary, J. P., & Smith, S. L. (2003). A four-dimensional validation of a coupled physical-biological model of the Arabian Sea. *Deep-Sea Research, part II*, *50*, 2917–2945.

Hopkins, T. L. (1982). The vertical distribution of zooplankton in the eastern Gulf of Mexico. *Deep Sea Research Part A. Oceanographic Research Papers*, *29*(9), 1069–1083. https://doi.org/10.1016/0198-0149(82)90028-0

Inoue, R., Kitamura, M., & Fujiki, T. (2016). Diel vertical migration of zooplankton at the S1 biogeochemical mooring revealed from acoustic backscattering strength. *Journal of Geophysical Research: Oceans*, *121*, 1031–1050. https://doi.org/10.1002/2015JC011352

Irigoien, X., Conway, D. V. P., & Harris, R. P. (2004). Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. *Marine Ecology Progress Series*, *267*, 85–97. https://doi.org/10.3354/meps267085

Isla, J. A., & Anadón, R. (2004). Mesozooplankton size-fractionated metabolism and feeding off NW Spain during autumn: Effects of a poleward current. *ICES Journal of Marine Science*, *61*(4), 526–534. https://doi.org/10.1016/j.icesjms.2004.03.014

Isla, A., Scharek, R., & Latasa, M. (2015). Zooplankton diel vertical migration and contribution to deep active carbon flux in the NW Mediterranean. *Journal of Marine Systems*, *143*, 86–97. https://doi.org/10.1016/j.jmarsys.2014.10.017

Jiang, S., Dickey, T. D., Steinberg, D. K., & Madin, L. P. (2007). Temporal variability of zooplankton biomass from ADCP backscatter time series data at the Bermuda Testbed Mooring site. *Deep Sea Research Part I: Oceanographic Research Papers*, *54*(4), 608–636. https://doi.org/10.1016/j.dsr.2006.12.011

Kaartvedt, S., Staby, A., & Aksnes, D. L. (2012). Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Marine Ecology Progress Series*, *456*, 1–6.

Kahru, M., & Mitchell, B. G. (2010). Blending of ocean colour algorithms applied to the southern ocean. *Remote Sensing Letters*, *1*(2), 119–124.

Kiørboe, T. (2011). How zooplankton feed: Mechanisms, traits and trade-offs. *Biological Reviews*, *86*(2), 311–339. https://doi.org/10.1111/j.1469-185X.2010.00148.x

Kitamura, M., Kobari, T., Honda, M. C., Matsumoto, K., Sasaoka, K., Nakamura, R., & Tanabe, K. (2016). Seasonal changes in the mesozooplankton biomass and community structure in subarctic and subtropical time-series stations in the western North Pacific. *Journal of Oceanography*, *72*(3), 387–402. https://doi.org/10.1007/s10872-015-0347-8

Kobari, T., Kitamura, M., Minowa, M., Isami, H., Akamatsu, H., Kawakami, H., et al. (2013). Impacts of the wintertime mesozooplankton community to downward carbon flux in the subarctic and subtropical Pacific Oceans. *Deep Sea Research Part I: Oceanographic Research Papers*, *81*, 78–88. https://doi.org/10.1016/j.dsr.2013.07.003

Kooijman, S. A. L. M. (2009). *Dynamic Energy Budget Theory for Metabolic Organisation*. Cambridge: Cambridge university press.

Korb, R. E., Whitehouse, M. J., & Ward, P. (2004). Seawifs in the southern ocean: Spatial and temporal variability in phytoplankton biomass around south georgia. *Deep-Sea Research, Part II*, *51*(1-3), 99–116.

Koslow, J. A., Kloser, R. J., & Williams, A. (1997). Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. *Marine Ecology Progress Series*, *146*, 21–35.

Lam, P., Lavik, G., Jensen, M. M., van de Vossenberg, J., Schmid, M., Woebken, D., et al. (2009). Revising the nitrogen cycle in the Peruvian oxygen minimum zone. *Proceedings of the National Academy of Sciences*, *106*(12), 4752–4757. https://doi.org/10.1073/pnas.0812444106

Lampert, W. (1989). The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology*, *3*(1), 21–27.

Landry, M. R., Al-Mutairi, H., Selph, K. E., Christensen, S., & Nunnery, S. (2001). Seasonal patterns of mesozooplankton abundance and biomass at Station ALOHA. *Deep Sea Research Part II: Topical Studies in Oceanography*, *48*(8), 2037–2061. https://doi.org/10.1016/S0967-0645(00)00172-7

Laws, E. A., Falkowski, P. G., Smith, W. O. Jr., Ducklow, H., & McCarthy, J. J. (2000). Temperature effects on export production in the open ocean. *Global Biogeochemical Cycles*, *14*, 1231–1246.

Le Borgne, R., Champalbert, G., & Gaudy, R. (2003). Mesozooplankton biomass and composition in the equatorial Pacific along 180°. *Journal of Geophysical Research*, *108*(C12), 8143. https://doi.org/10.1029/2000JC000745

Le Mézo, P., Lefort, S., Séférian, R., Aumont, O., Maury, O., Murtugudde, R., & Bopp, L. (2016). Natural variability of marine ecosystems inferred from a coupled climate to ecosystem simulation. *Journal of Marine Systems*, *153*, 55–66. https://doi.org/10.1016/j.jmarsys.2015.09.004

Lee, C. M., Jones, B. H., Brink, K. H., & Fischer, A. S. (2000). The upper-ocean response to monsoonal forcing in the arabian sea: Seasonal and spatial variability. *Deep-Sea Research, part II*, *47*, 1177–1226.

Lefort, S., Aumont, O., Bopp, L., Arsouze, T., Gehlen, M., & Maury, O. (2015). Spatial and body-size dependent response of marine pelagic communities to projected global climate change. *Global Change Biology*, *21*(1), 154–164. https://doi.org/10.1111/gcb.12679

Longhurst, A. R., Bedo, A., Harrison, W. G., Head, E. J. H., Horne, E. P., Irwin, B., & Morales, C. (1989). NFLUX: A test of vertical nitrogen flux by diel migrant biota. *Deep Sea Research Part A. Oceanographic Research Papers*, *36*(11), 1705–1719. https://doi.org/10.1016/0198-0149(89)90067-8

Longhurst, A. R., & Glen Harrison, W. (1988). Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. *Deep Sea Research Part A. Oceanographic Research Papers*, *35*(6), 881–889. https://doi.org/10.1016/0198-0149(88)90065-9

Loose, C. J., & Dawidowicz, P. (1994). Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. *Ecology*, *75*(8), 2255–2263. https://doi.org/10.2307/1940881

Loose, C. J., Von Elert, E., & Dawidowicz, P. (1993). Chemically-induced diel vertical migration in Daphnia: A new bioassay for kairomones exuded by fish. *Archiv für Hydrobiologie*, *126*(3), 329–337.

Luo, J., Ortner, P. B., Forucci, D., & Cummings, S. R. (2000). Diel vertical migration of zooplankton and mesopelagic fish in the arabian sea. *Deep-Sea Research II*, *47*, 1451–1473.

Lutz, M. J., Caldeira, K., Dunbar, R. B., & Behrenfeld, M. J. (2007). Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. *Journal of Geophysical Research*, *112*, C10011. https://doi.org/10.1029/2006JC003706

Madec, G. (2008). "NEMO ocean engine", *Note du Pôle de Modélisation 27*. France: Institut Pierre-Simon Laplace (IPSL).

Madhupratap, M., Gopalakrishnan, T. C., Haridas, P., & Nair, K. K. C. (2001). Mesozooplankton biomass, composition and distribution in the Arabian Sea during the Fall Intermonsoon: Implications of oxygen gradients. *Deep Sea Research Part II: Topical Studies in Oceanography*, *48*(6), 1345–1368. https://doi.org/10.1016/S0967-0645(00)00142-9

Madin, L. P., Horgan, E. F., & Steinberg, D. K. (2001). Zooplankton at the Bermuda Atlantic Time-series Study (BATS) station: Diel, seasonal and interannual variation in biomass, 1994-1998. *Deep Sea Research Part II: Topical Studies in Oceanography*, *48*(8), 2063–2082. https://doi.org/10.1016/S0967-0645(00)00171-5

Marlowe, C. J., & Miller, C. B. (1975). Patterns of vertical distribution and migration of zooplankton at Ocean Station "P"1. *Limnology and Oceanography*, *20*(5), 824–844. https://doi.org/10.4319/lo.1975.20.5.0824

Martin, B., & Christiansen, B. (2009). Distribution of zooplankton biomass at three seamounts in the NE Atlantic. *Deep Sea Research Part II: Topical Studies in Oceanography*, *56*(25), 2671–2682. https://doi.org/10.1016/j.dsr2.2008.12.026

Maury, O. (2010). An overview of APECOSM, a spatialized mass balanced "Apex Predators ECOSystem Model" to study physiologically structured tuna population dynamics in their ecosystem. *Progress in Oceanography*, *84*(1–2), 113–117. https://doi.org/10.1016/j.pocean.2009.09.013

Maury, O., Faugeras, B., Shin, Y.-J., Poggiale, J.-C., Ben Ari, T., & Marsac, F. (2007). Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 1: The model. *Progress in Oceanography*, *74*(4), 479–499.

Miljeteig, C., Olsen, A. J., Båtnes, A. S., Altin, D., Nordtug, T., Alver, M. O., et al. (2014). Sex and life stage dependent phototactic response of the marine copepod Calanus finmarchicus (Copepoda: Calanoida). *Journal of Experimental Marine Biology and Ecology*, *451*(Supplement C), 16–24. https://doi.org/10.1016/j.jembe.2013.10.032

Moore, A. R. (1912). Concerning negative phototropism in Daphnia pulex. *Journal of Experimental Zoology*, *13*(4), 573–575. https://doi.org/10.1002/jez.1400130403

Moriarty, R., Buitenhuis, E. T., Quéré, C. L., & Gosselin, M.-P. (2013). Distribution of known macrozooplankton abundance and biomass in the global ocean. *Earth System Science Data*, *5*(2), 241–257. https://doi.org/10.5194/essd-5-241-2013

Moriarty, R., & O'Brien, T. D. (2013). Distribution of mesozooplankton biomass in the global ocean. *Earth System Science Data*, *5*(1), 45–55. https://doi.org/10.5194/essd-5-45-2013

Morozov, A. Y., & Kuzenkov, O. A. (2016). Towards developing a general framework for modelling vertical migration in zooplankton. *Journal of Theoretical Biology*, *405*, 17–28. https://doi.org/10.1016/j.jtbi.2016.01.011

Murray, J., & Hjort, J. (1912). *The Depths of the Ocean* (pp. 821). London: McMillan.

Najjar, R. G., Jin, X., Louanchi, F., Aumont, O., Caldeira, K., Doney, S. C., et al. (2007). Impact of circulation on export production, dissolved organic matter, and dissolved oxygen in the ocean: Results from Phase II of the Ocean Carbon-cycle Model Intercomparison Project (OCMIP-2). *Global Biogeochemical Cycles*, *21*, GB3007. https://doi.org/10.1029/2006GB002857

Neill, W. E. (1990). Induced vertical migration in copepods as a defence against invertebrate predation. *Nature*, *345*, 524–526. https://doi.org/10.1038/345524a0

Ohman, M. D., Frost, B. W., & Cohen, E. B. (1983). Reverse diel vertical migration: An escape from invertebrate predators. *Science*, *220*(4604), 1404–1407.

Packard, T. T., & Gómez, M. (2013). Modeling vertical carbon flux from zooplankton respiration. *Progress in Oceanography*, *110*, 59–68. https://doi.org/10.1016/j.pocean.2013.01.003

Pal, I. K., Terdalkar, S., & Pereira, M. L. (2010). Zooplankton diel vertical migration in Andaman Sea. In R. C. Ramakrishna & C. Sivaperuman *Recent Trends in Biodiversity of Andaman and Nicobar Islands* (Vol. 7, pp. 113–129) Kolkata, India: Zoological Survey of India.

Pangle, K. L., & Peacor, S. D. (2006). Non-lethal effect of the invasive predator Bythotrephes longimanus on Daphnia mendotae. *Freshwater Biology*, *51*(6), 1070–1078. https://doi.org/10.1111/j.1365-2427.2006.01555.x

Perissinotto, R., & McQuaid, C. D. (1992). Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Marine Ecology Progress Series*, *20*, 15–27.

Pinot, J. M., & Jansá, J. (2001). Time variability of acoustic backscatter from zooplankton in the Ibiza Channel (western Mediterranean). *Deep Sea Research Part I: Oceanographic Research Papers*, *48*(7), 1651–1670. https://doi.org/10.1016/S0967-0637(00)00095-9

Piontkovski, S. A., & Williams, R. (1995). Multiscale variability of tropical ocean zooplankton biomass. *ICES Journal of Marine Science*, *52*(3-4), 643 – 656. https://doi.org/10.1016/1054-3139(95)80078-6

Putzeys, S., Yebra, L., Almeida, C., Bécognée, P., & Hernández-León, S. (2011). Influence of the late winter bloom on migrant zooplankton metabolism and its implications on export fluxes. *Journal of Marine Systems*, *88*(4), 553 – 562. https://doi.org/10.1016/j.jmarsys.2011.07.005

Resplandy, L., Lévy, M., Madec, G., Pous, S., Aumont, O., & Kumar, D. (2011). Contribution of mesoscale processes to nutrient budgets in the Arabian Sea. *Journal of Geophysical Research*, *116*, C11007. https://doi.org/10.1029/2011JC007006

Ringelberg, J. (1995). Changes in light intensity and diel vertical migration: A comparison of marine and freshwater environments. *Journal of the Marine Biological Association of the United Kingdom*, *75*(1), 15 – 25. https://doi.org/10.1017/S0025315400015162

Ringelberg, J., & Gool, E. V. (2003). On the combined analysis of proximate and ultimate aspects in diel vertical migration (DVM) research. *Hydrobiologia*, *491*(1-3), 85 – 90. https://doi.org/10.1023/A:1024407021957

Rodier, M., & Le Borgne, R. (1997). Export flux of particles at the equator in the western and central Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, *44*(9), 2085 – 2113. https://doi.org/10.1016/S0967-0645(97)00092-1

Roman, M. R., Dam, H. G., Le Borgne, R., & Zhang, X. (2002). Latitudinal comparisons of equatorial Pacific zooplankton. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*(13), 2695 – 2711. https://doi.org/10.1016/S0967-0645(02)00054-1

Rose, K. A., Allen, J. I., Artioli, Y., Barange, M., Blackford, J., Carlotti, F., et al. (2010). End-to-end models for the analysis of marine ecosystems: Challenges, issues, and next steps. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, *2*, 115 – 130. https://doi.org/10.1577/C09-059.1

Sainmont, J., Thygesen, U. H., & Visser, A. W. (2013). Diel vertical migration arising in a habitat selection game. *Theoretical Ecology*, *6*(2), 241 – 251. https://doi.org/10.1007/s12080-012-0174-0

Schukat, A., Bode, M., Auel, H., Carballo, R., Martin, B., Koppelmann, R., & Hagen, W. (2013). Pelagic decapods in the northern Benguela upwelling system: Distribution, ecophysiology and contribution to active carbon flux. *Deep Sea Research Part I: Oceanographic Research Papers*, *75*, 146 – 156. https://doi.org/10.1016/j.dsr.2013.02.003

Seibel, B. A. (2011). Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *Journal of Experimental Biology*, *214*(2), 326 – 336. https://doi.org/10.1242/jeb.049171

Shea, E. K., & Vecchione, M. (2010). Ontogenic changes in diel vertical migration patterns compared with known allometric changes in three mesopelagic squid species suggest an expanded definition of a paralarva. *ICES Journal of Marine Science*, *67*(7), 1436 – 1443. https://doi.org/10.1093/icesjms/fsq104

Shimode, S., Hiroe, Y., Hidaka, K., Takahashi, K., & Tsuda, A. (2009). Life history and ontogenetic vertical migration of Neocalanus gracilis in the western North Pacific Ocean. *Aquatic Biology*, *7*(3), 295 – 306.

Siegel, D. A., Buesseler, K. O., Doney, S. C., Sailley, S. F., Behrenfeld, M. J., & Boyd, P. W. (2014). Global assessment of ocean carbon export by combining satellite observations and food-web models. *Global Biogeochemical Cycles*, *28*, 181 – 196. https://doi.org/10.1002/2013GB004743

Smeti, H., Pagano, M., Menkes, C., Lebourges-Dhaussy, A., Hunt, B. P. V., Allain, V., et al. (2015). Spatial and temporal variability of zooplankton off New Caledonia (Southwestern Pacific) from acoustics and net measurements. *Journal of Geophysical Research: Oceans*, *120*, 2676 – 2700. https://doi.org/10.1002/2014JC010441

Smith, S., Roman, M., Prusova, I., Wishner, K., Gowing, M., Codispoti, L. A., et al. (1998). Seasonal response of zooplankton to monsoonal reversals in the Arabian Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, *45*(10), 2369 – 2403. https://doi.org/10.1016/S0967-0645(98)00075-7

Steinberg, D. K., Carlson, C. A., Bates, N. R., Goldthwait, S. A., Madin, L. P., & Michaels, A. F. (2000). Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, *47*(1), 137 – 158. https://doi.org/10.1016/S0967-0637(99)00052-7

Steinberg, D. K., Cope, J. S., Wilson, S. E., & Kobari, T. (2008). A comparison of mesopelagic mesozooplankton community structure in the subtropical and subarctic North Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, *55*(14), 1615 – 1635. https://doi.org/10.1016/j.dsr2.2008.04.025

Steinberg, D. K., Van Mooy, B. A. S., Buesseler, K. O., Boyd, P. W., Kobari, T., & Karl, D. M. (2008). Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnology and Oceanography*, *53*(4), 1327 – 1338. https://doi.org/10.4319/lo.2008.53.4.1327

Stramma, L., Prince, E. D., Schmidtko, S., Luo, J., Hoolihan, J. P., Visbeck, M., et al. (2012). Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change*, *2*(1), 33 – 37. https://doi.org/10.1038/nclimate1304

Stukel, M. R., Ohman, M. D., Benitez-Nelson, C. R., & Landry, M. R. (2013). Contributions of mesozooplankton to vertical carbon export in a coastal upwelling system. *Marine Ecology Progress Series*, *491*, 47 – 65.

Stupnikova, A. N., & Vereshchaka, A. L. (2013). High-resolution survey indicates high heterogeneity in copepod distribution in the hydrologically active Drake Passage. *Journal of Natural History*, *47*(5-12), 699 – 713. https://doi.org/10.1080/00222933.2012.708451

Takahashi, T., Broecker, W. S., & Langer, S. (1985). Redfield ratio based on chemical data from isopycnal surfaces. *Journal of Geophysical Research*, *90*, 6907 – 6924.

Takahashi, K., Kuwata, A., Sugisaki, H., Uchikawa, K., & Saito, H. (2009). Downward carbon transport by diel vertical migration of the copepods Metridia pacifica and Metridia okhotensis in the Oyashio region of the western subarctic Pacific Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, *56*(10), 1777 – 1791. https://doi.org/10.1016/j.dsr.2009.05.006

Timmermann, R., Goose, H., Madec, G., Fichefet, T., Ethé, C., & Dulière, V. (2005). On representation of high latitude processes in the ORCALIM global coupled sea ice-ocean model. *Ocean Modelling*, *8*, 175 – 201.

Timonin, A. G. (1995). Diurnal dynamics of the plankton distribution in the northern Benguela upwelling system. *Oceanology of the Russian Academy of Sciences*, *35*(4), 511 – 515.

Ward, P., Atkinson, A., Murray, A. W. A., Wood, A. G., Williams, R., & Poulet, S. A. (1995). The summer zooplankton community at South Georgia: Biomass, vertical migration and grazing. *Polar Biology*, *15*(3), 195 – 208. https://doi.org/10.1007/BF00239059

Wishner, K. F., Ashjian, C. J., Gelfman, C., Gowing, M. M., Kann, L., Levin, L. A., et al. (1995). Pelagic and benthic ecology of the lower interface of the Eastern Tropical Pacific oxygen minimum zone. *Deep Sea Research Part I: Oceanographic Research Papers*, *42*(1), 93 – 115. https://doi.org/10.1016/0967-0637(94)00021-J

Yamaguchi, A., Onishi, Y., Kawai, M., Omata, A., Kaneda, M., & Ikeda, T. (2010). Diel and ontogenetic variations in vertical distributions of large grazing copepods during the spring phytoplankton bloom in the Oyashio region. *Deep Sea Research Part II: Topical Studies in Oceanography*, *57*(17), 1691 – 1702. https://doi.org/10.1016/j.dsr2.2010.03.013

Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., et al. (2002). Structure and size distribution of plankton communities down to the greater depths in the western North Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*(24), 5513–5529. https://doi.org/10.1016/S0967-0645(02)00205-9

Yebra, L., Hernández-León, S., Almeida, C., & Bécognée, P. (2009). Metabolism and biomass vertical distribution of zooplankton in the Bransfield Strait during the austral summer of 2000. *Polar Research*, *28*(3), 415–425. https://doi.org/10.1111/j.1751-8369.2009.00116.x

Zaret, T. M., & Suffern, J. S. (1976). Vertical migration in zooplankton as a predator avoidance mechanism. *Limnology and Oceanography*, *21*(6), 804–813.

Zhang, X., & Dam, H. G. (1997). Downward export of carbon by diel migrant mesozooplankton in the central equatorial Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography*, *44*(9), 2191–2202. https://doi.org/10.1016/S0967-0645(97)00060-X