



A high-resolution modeling study on diel and seasonal vertical migrations of high-latitude copepods



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ABSTRACT

Despite diel and seasonal vertical migrations (DVM and SVM) of high-latitude zooplankton have been studied since the late-19th century, questions still remain about the influence of environmental seasonality on vertical migration, and the combined influence of DVM and SVM on zooplankton fitness. Toward addressing these, we developed a model for simulating DVM and SVM of high-latitude herbivorous copepods in high spatio-temporal resolution. In the model, a unique timing and amplitude of DVM and SVM and its ontogenetic trajectory were defined as a vertical strategy. Growth, survival and reproductive performances of numerous vertical strategies hardwired to copepods spawned in different times of the year were assessed by a fitness estimate, which was heuristically maximized by a Genetic Algorithm to derive the optimal vertical strategy for a given model environment. The modelled food concentration, temperature and visual predation risk had a significant influence on the observed vertical strategies. Under low visual predation risk, DVM was less pronounced, and SVM and reproduction occurred earlier in the season, where capital breeding played a significant role. Reproduction was delayed by higher visual predation risk, and copepods that spawned later in the season used the higher food concentrations and temperatures to attain higher growth, which was efficiently traded off for survival through DVM. Consequently, the timing of SVM did not change much from that predicted under lower visual predation risk, but the body and reserve sizes of overwintering stages and the importance of capital breeding diminished. Altogether, these findings emphasize the significance of DVM in environments with elevated visual predation risk and shows its contrasting influence on the phenology of reproduction and SVM, and moreover highlights the importance of conducting field and modeling work to study these migratory strategies in concert.

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1. Introduction

Vertical migration is a common behavior of many zooplankton taxa. Based on the periodicity, vertical migrations of high-latitude zooplankton are classified into diel and seasonal components, which have been studied since the late-19th century (reviewed in Russell, 1927; Cushing, 1951; Banse, 1964). The short-term diel vertical migration (DVM) has a periodicity of up to 24 h, and is understood as a strategy that trades off growth potential to reduce the mortality risk imposed by visual predators (Lampert, 1989;

Ohman, 1990; Loose and Dawidowicz, 1994). The long-term seasonal vertical migration (SVM) has a periodicity of up to one year, and reflects adaptations to seasonal extremities of food availability (Head and Harris, 1985; Hind et al., 2000; Bandara et al., 2016), temperature (Hirche, 1991; Astthorsson and Gislason, 2003) and predation risk (Kaartvedt, 1996; Bagøien et al., 2000; Varpe and Fiksen, 2010). In either case, since both DVM and SVM can alter feeding, growth, survival and reproduction, and ultimately affect fitness (Aidley, 1981; Alerstam et al., 2003; Cresswell et al., 2011; Litchman et al., 2013), these migratory strategies are termed vertical strategies (Bandara et al., 2016).

Empirical knowledge on zooplankton vertical strategies largely comes from studying the dynamic vertical positioning of populations in a water column, and are often rather coarse in spatial (vertical) and temporal resolution (Pearre, 1979). This can undermine the key concept that such migrations are individual responses

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Table 1
Some endogenous and exogenous cues that are believed to proximately or ultimately regulate diel and seasonal vertical migrations of marine and freshwater zooplankton. Literature do not come from an exhaustive review and only serve as examples.

Cue	DVM	SVM
Temperature	McLaren (1963), Enright (1977)	Hirche (1991), Heath and Jónasdóttir (1999), Astthorsson and Gislason (2003)
Light (absolute or relative irradiance from sun, moon, stars, or aurora borealis, photoperiod, spectral quality, polarization etc.)	Clarke (1933), Gliwicz (1986), Frank and Widder (1997), Berge et al. (2009), Båtnes et al. (2015), Cohen et al. (2015), Bianchi and Mislan (2016), Bozman et al. (2017)	Sømme (1934), Ussing (1938), Miller et al. (1991)
Dissolved oxygen	Devol (1981), Bianchi et al. (2013)	–
Water depth, transparency and UV radiation	Rhode et al. (2001), Williamson et al. (2011), Ekvall et al. (2015)	Dupont and Aksnes (2012)
Tides, currents and advective transport	Hardy (1935), Wroblewski (1982), Kimmerer and McKinnon (1987)	Berge et al. (2012), Irigoien (2004)
Food availability	Hardy and Gunther (1935), Huntley and Brooks (1982), George (1983), Johnsen and Jakobsen (1987)	Herman (1983), Hind et al. (2000), Head and Harris (1985), Bandara et al. (2016)
Visual and tactile predation	Zaret and Suffern (1976), Iwasa (1982), Ohman (1990), Bollens et al. (1992), Loose and Dawidowicz (1994)	Kaartvedt (1996), Kaartvedt (2000), Dale et al. (1999), Bagoien et al. (2000), Varpe and Fiksen (2010)
Body size, ontogeny and pigmentation	Zaret and Kerfoot (1975), Uye et al. (1990), Hays et al. (1994), Dale and Kaartvedt (2000)	Østvedt (1955), Hind et al. (2000)
Nutritional state and lipid reserves	Fiksen and Carlotti (1998), Sekino and Yamamura (1999)	Visser and Jónasdóttir (1999), Thorisson (2006)
Endogenous rhythms and internal biological clocks	Cohen and Forward (2009), van Haren and Compton (2013)	Carlisle and Pitman (1961), Miller et al. (1991), Hirche (1996)

to certain cues or stimuli and not a property of the population (Zink, 2002), and may complicate the understanding of the relationships between vertical strategies and environmental variables (see Table 1 for examples). Moreover, since diel and seasonal vertical migrations occur on different spatial and temporal scales, studying these migrations together in the field in adequate resolution remains a major challenge. Although novel optical and acoustic methods of *in-situ* observation offer a solution to some of these problems (e.g. Basedow et al., 2010; Sainmont et al., 2014b; Bozman et al., 2017; Darnis et al., 2017), long-term deployment and accurately resolving the identity of the migrants remain as key challenges.

Mechanistic models offer an alternative means of studying zooplankton vertical strategies in higher resolution. Models related to DVM usually encompass the highest spatial (≤ 1 m), temporal (≤ 1 h) and biological (=individual) resolution (e.g. Fiksen and Giske, 1995; Eiane and Parisi, 2001; Liu et al., 2003; Burrows and Tarling, 2004; Hansen and Visser, 2016). Models related to SVM and diapause (i.e. hibernation in deeper waters, e.g. Hirche, 1996) encompass the same biological resolution, but are usually coarse in spatio-temporal resolution. Here, the time intervals range from 1 h to 1d and vertical spatial elements are usually resolved to either absolute depth units (e.g. 1 m bins) or segregated habitats (e.g. Fiksen and Carlotti, 1998; Miller et al., 1998; Hind et al., 2000; Ji, 2011; Ji et al., 2012; Sainmont et al., 2015; Banas et al., 2016). The choice of a coarser spatio-temporal resolution of these models reflects the broader space and time scales at which the SVM and diapause occurs. This contrasting spatio-temporal scale makes it difficult to harbor lifetime dynamics of DVM to be simulated in SVM models without significantly increasing computer time. Consequently, most models that simulate SVM tend to either fully (e.g. Hind et al., 2000) or partly (i.e. of younger developmental stages, e.g. Fiksen and Carlotti, 1998) disregard DVM. However, the validity of such simplifications are questionable, given the geographically and taxonomically widespread nature of zooplankton DVM behavior and its ontogenetic patterns (Huntley and Brooks, 1982; Huang et al., 1993; Osgood and Frost, 1994; Hays, 1995). It is thus interesting to investigate whether the extra biological information resulting from modeling DVM and SVM in concert is a worthy trade-off for the elevated computer time. If so, such models may lead to improvements of the current understanding about how environmental seasonal-

Table 2

Evolvable (soft) parameters optimized in the model. The first six are proxies that define the vertical strategy. Vertical strategies of copepods spawned in different times of the year (t_B) are optimized using the GA.

Term	Definition	Range	Interval	Unit
α	Light sensitivity parameter	$0-I_{\max}^a$	1	$\mu\text{mol m}^{-2} \text{s}^{-1}$
β	Size-specificity of light sensitivity parameter	0–10	1	dim.less
γ	Growth allocation parameter	0–1	0.01	dim.less
δ	Seasonal descent parameter	0–1	0.01	dim.less
ζ	Overwintering depth	1–500	10	m
ε	Seasonal ascent parameter	0–1	0.01	dim.less
t_B	Time of birth ^b	1–8760	1	h

^a The upper limit of α changes with the maximum surface irradiance of the model environment, i.e. $I_{\max} = 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ for Environment-L, $1300 \mu\text{mol m}^{-2} \text{s}^{-1}$ for Environment-M and $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ for Environment-H (cf. Fig. 1).

^b Time of being spawned.

ity shapes up vertical strategies, and the means of which the latter influences life histories of high latitude zooplankton.

In this study, we present a model of zooplankton vertical strategies. The model operates in a high-latitude setting and simulates both DVM and SVM of a herbivorous copepod with an annual life cycle in high spatial (vertical) and temporal resolution. Using this model, we aim to investigate the influence of environmental variables on vertical strategies, and how vertical strategies affect fitness and phenology in seasonal environments. We further discuss how short-term behavior (DVM) influences and interacts in the longer-term and shape-up different life history components of copepod strategies.

2. Materials and methods

Although the model is not strictly individual-based, it is described following the Overview, Design concepts and Details (ODD) protocol (Grimm et al., 2006, 2010) to improve reproducibility.

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