BIOLOGICAL REVIEWS
Cambridge Philosophical Society
Biol. Rev. (2021), **96**, pp. 1547–1589.
doi: 10.1111/brv.12715

Two hundred years of zooplankton vertical migration research

Kanchana Bandara[1,2*], Øystein Varpe[3,4], Lishani Wijewardene[5], Vigdis Tverberg[1] and Ketil Eiane[1]

[1]*Faculty of Biosciences and Aquaculture, Nord University, 8049, Bodø, Norway*
[2]*Department of Arctic and Marine Biology, Faculty of Fisheries, Biosciences and Economics, UiT–The Arctic University of Norway, 9037, Tromsø, Norway*
[3]*Department of Biological Sciences, University of Bergen, 5020, Bergen, Norway*
[4]*Norwegian Institute for Nature Research, 5006, Bergen, Norway*
[5]*Department of Hydrology and Water Resources Management, Institute of Natural Resource Conservation, Kiel University, 24118, Kiel, Germany*

ABSTRACT

Vertical migration is a geographically and taxonomically widespread behaviour among zooplankton that spans across diel and seasonal timescales. The shorter-term diel vertical migration (DVM) has a periodicity of up to 1 day and was first described by the French naturalist Georges Cuvier in 1817. In 1888, the German marine biologist Carl Chun described the longer-term seasonal vertical migration (SVM), which has a periodicity of *ca.* 1 year. The proximate control and adaptive significance of DVM have been extensively studied and are well understood. DVM is generally a behaviour controlled by ambient irradiance, which allows herbivorous zooplankton to feed in food-rich shallower waters during the night when light-dependent (visual) predation risk is minimal and take refuge in deeper, darker waters during daytime. However, DVMs of herbivorous zooplankton are followed by their predators, producing complex predator–prey patterns that may be traced across multiple trophic levels. In contrast to DVM, SVM research is relatively young and its causes and consequences are less well understood. During periods of seasonal environmental deterioration, SVM allows zooplankton to evacuate shallower waters seasonally and take refuge in deeper waters often in a state of dormancy. Both DVM and SVM play a significant role in the vertical transport of organic carbon to deeper waters (biological carbon sequestration), and hence in the buffering of global climate change. Although many animal migrations are expected to change under future climate scenarios, little is known about the potential implications of global climate change on zooplankton vertical migrations and its impact on the biological carbon sequestration process. Further, the combined influence of DVM and SVM in determining zooplankton fitness and maintenance of their horizontal (geographic) distributions is not well understood. The contrasting spatial (deep *versus* shallow) and temporal (diel *versus* seasonal) scales over which these two migrations occur lead to challenges in studying them at higher spatial, temporal and biological resolution and coverage. Extending the largely population-based vertical migration knowledge base to individual-based studies will be an important way forward. While tracking individual zooplankton in their natural habitats remains a major challenge, conducting trophic-scale, high-resolution, year-round studies that utilise emerging field sampling and observation techniques, molecular genetic tools and computational hardware and software will be the best solution to improve our understanding of zooplankton vertical migrations.

Key words: diel vertical migration, seasonal vertical migration, proximate cues, adaptive significance, vertical habitat choice, zooplankton sampling methods, climate change, resting stages

CONTENTS

I. Introduction 1548
II. Diel vertical migration of zooplankton 1549

* Address for correspondence (Tel: +4746257006, +4793284723; E-mail: info@kanchanabandara.com)

Biological Reviews **96** (2021) 1547–1589 © 2021 The Authors. *Biological Reviews* published by John Wiley & Sons Ltd on behalf of Cambridge Philosophical Society. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

(1) Control mechanisms . . . 1550
(a) *Hypotheses about the proximate control of DVM* . . . 1550
(b) *Hypotheses about the adaptive significance of DVM* . . . 1552
(2) Plasticity of DVM . . . 1553
(3) Costs and risks of DVM . . . 1553
(4) Community and ecosystem consequences of DVM . . . 1554
III. Seasonal vertical migration of zooplankton . . . 1555
(1) Low-amplitude SVM of resting stages . . . 1557
(a) *SVM of embryonic resting stages* . . . 1557
(b) *SVM of non-embryonic resting stages* . . . 1558
(2) High-amplitude SVM of overwintering and oversummering stages . . . 1558
(a) *SVM in high-latitude environments* . . . 1559
(b) *SVM in upwelling environments* . . . 1560
(3) Control mechanisms . . . 1560
(a) *Hypotheses about the proximate control of SVM* . . . 1560
(i) *Hypotheses about seasonal descent and diapause induction* . . . 1560
(ii) *Hypotheses about diapause termination and seasonal ascent* . . . 1562
(iii) *Hypotheses about migration amplitude (vertical habitat selection)* . . . 1564
(b) *Hypotheses about the adaptive significance of SVM* . . . 1564
(4) Plasticity of SVM . . . 1565
(5) Community and ecosystem consequences of SVM . . . 1566
IV. Methods of studying zooplankton vertical migrations . . . 1566
(1) Sampling methods . . . 1566
(a) *Sampling in marine systems* . . . 1567
(b) *Sampling in freshwater systems* . . . 1567
(2) *In-situ* observation methods . . . 1568
(a) *Acoustic observations* . . . 1568
(i) *Acoustic observations in marine systems* . . . 1568
(ii) *Acoustic observations in freshwater systems* . . . 1569
(b) *Optical techniques* . . . 1569
(3) Tracking and simulation methods . . . 1569
(a) *Tracking vertical migrations of individuals* . . . 1569
(b) *Simulating vertical migrations of virtual individuals* . . . 1570
V. Challenges, opportunities and directions for future research . . . 1571
(1) Improving the quality of zooplankton vertical distribution data . . . 1571
(a) *Strategies to improve data resolution* . . . 1571
(b) *Strategies to improve data coverage* . . . 1571
(2) The need to broaden SVM research . . . 1572
(3) The importance of studying DVM and SVM in concert . . . 1573
(4) Vertical migration and climate change . . . 1574
(5) From genes to ecosystems: the importance of integrated and collaborative approaches . . . 1575
VI. Conclusions . . . 1576
VII. Acknowledgements . . . 1576
VIII. References . . . 1576

I. INTRODUCTION

Migration involves persistent and active movement of animals typically from one habitat to another and is often caused by spatial and temporal variation of resources and risks (Aidley, 1981; Cresswell, William & Sword, 2011). Through migration, individuals may elevate the likelihood of encountering opportunities of feeding and growth (e.g. L'Abée-Lund & Vøllestad, 1987; Williamson, Williamson & Ngwamotsoko, 1988; Levey & Stiles, 1992), survival (e.g. Werner *et al.*, 1983; Hebblewhite & Merrill, 2007; McKinnon *et al.*, 2010) and reproduction (e.g. Hardy & Raymond, 1980; Smith & Moore, 2005; van Ginneken & Maes, 2005). As a result, migrants may enhance their fitness compared to non-migrants, assuming that the benefits of the migration outweigh the costs (Aidley, 1981).

An accurate description of migration usually requires tracking the displacement of migrants across longitudes, latitudes and altitude or depth over time. However, defining migration as a movement between habitats allows migratory trajectories to be simplified into one or two spatial dimensions along which the migratory habitats exist (Southwood, 1962; Dingle & Drake, 2007). In this regard, migratory trajectories of most terrestrial, aquatic and avian

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

animals are usually described using two-dimensional geographic coordinate systems that disregard the vertical dimension (e.g. Wallace *et al.*, 2003; Block *et al.*, 2005; Egevang *et al.*, 2010). The vertical trajectory of the migration becomes significant when migrants exert pronounced diving or flying behaviour during their excursions (e.g. Weng *et al.*, 2007; Hawkes *et al.*, 2011). For some animal migrations, depth is the only behaviourally controlled (active) component and hence the sole descriptor of the migratory trajectory. These 'vertical migrations' are widespread among zooplankton that swim up and down the water column (reviewed in Russell, 1927; Cushing, 1951; Banse, 1964).

The concept of zooplankton vertical migration originated in the 19th century, based on the observations of periodic appearance and disappearance of pelagic crustaceans from near-surface waters of freshwater lakes (Cuvier, 1817) and oceans (Schmidtlein, 1879). Field investigations conducted in the late 19th century indicated that these periodic patterns are a result of zooplankton actively migrating through the water column (Fuchs, 1882; Chun, 1888). Consequently, the term 'vertical migration' was established in the literature by the early 20th century. Due to the difficulty of tracking individual zooplankton across space and time, much of the current evidence for zooplankton vertical migrations come from observing vertical changes of zooplankton population centres over time. The predictions and interpretations of zooplankton vertical behaviour from population observations are more accurate at higher population sizes and especially when vertical behaviours among individuals are largely synchronous (Pearre, 1979). However, asynchronous vertical migrations also exist among zooplankton populations (e.g. Cottier *et al.*, 2006) and likely signify among-individual variability of the migratory behaviour.

Russell (1927) classified zooplankton vertical migrations based on the timing of the migration (periodicity), areas over which it takes place (e.g. geographical regions and spawning habitats) and biological attributes, such as ontogeny and sex. His classification based on the migration periodicity remains the most prominent today, and accordingly, two types of vertical migrations exist: the shorter-term diel vertical migration (DVM) with a periodicity of up to 1 day and the longer-term seasonal vertical migration (SVM) with a periodicity of up to 1 year. In general, DVM represents the widespread tendency of zooplankton to occupy deeper waters during the day and near-surface waters during the night (Hays, 2003; Brierley, 2014). Unlike DVM, SVM is largely confined to seasonal environments, such as high-latitude aquatic habitats (reviewed in Conover, 1988; Falk-Petersen *et al.*, 2009) and upwelling systems (reviewed in Peterson, 1998; Teuber *et al.*, 2019) and reflects the tendency of zooplankton to occupy various vertical habitats during different times of the year. Since the vertical distribution of the migrants usually varies across developmental stages, SVM is often described as an ontogenetic vertical migration (Peterson, Miller & Hutchinson, 1979; Schnack-Schiel & Hagen, 1994; Madhupratap, Nehring & Lenz, 1996; Makabe *et al.*, 2016). Despite the generality of the above classification, reverse diel and seasonal vertical migrations also exist (e.g. Ohman, Frost & Cohen, 1983; Schnack-Schiel & Hagen, 1995).

Since the pioneering work of Cuvier (1817), studies of zooplankton vertical migrations have developed into a rapidly growing field of study rich in empirical and theoretical advances, which range from the level of individuals to communities and ecosystems (reviewed in Hays, 2003; Brierley, 2014; Dawidowicz & Pijanowska, 2018). However, there are still opportunities for broadening our understanding of the causes and consequences of zooplankton vertical migrations. We therefore aim this synthesis towards reviewing some of the key discoveries that led to or have the potential of leading to an improved understanding of zooplankton vertical migrations. Although zooplankton are a diverse group of organisms with a broad range of body sizes, this synthesis mainly focuses on mesozooplankton (0.2–20 mm; Sieburth, Smetacek & Lenz, 1978). Since boundaries between zooplankton size groups are vague, some discussions may include larger microzooplankton (<0.2 mm) and smaller macrozooplankton (>20 mm). Orientating on the classification of vertical migrations based on periodicity (Russell, 1927), we focus on both diel and seasonal vertical migrations and (*i*) revisit the historical events that led to the discovery of these migrations, (*ii*) describe hypotheses about its proximate control (i.e. how migration occurs) and adaptive significance (why migration exists) with an attempt to trace the historical background of these hypotheses, (*iii*) discuss the methods used to study vertical migrations and (*iv*) highlight challenges and opportunities, and provide directions for future research.

II. DIEL VERTICAL MIGRATION OF ZOOPLANKTON

In *Le Règne Animal* (The Animal Kingdom), Cuvier (1817) made what is probably the first written record of zooplankton DVM. In a clear shallow freshwater lake, he noted *Daphnia* retreating to deeper waters during midday and ascending back to near-surface waters in the evening. However, diel migrations of zooplankton in deeper lakes and the open ocean were not studied in detail at the time, probably due to the lack of appropriate sampling techniques to trace relatively deep vertical movements of planktonic animals. This limitation was addressed in the late 19th century, when the Austrian geologist Theodor Fuchs used depth-stratified net samples and showed that the daytime disappearance of marine pelagic crustaceans from near-surface waters was due to their retreat to deeper layers (Fuchs, 1882).

DVM is a widespread behaviour among many freshwater and marine zooplankton taxa across all latitudes, and it is one of the most-studied patterns of animal behaviour (Hays, 2003; Dawidowicz & Pijanowska, 2018). The most common form of DVM is the nocturnal DVM, which involves a night-time ascent to the upper pelagial and a

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

daytime descent to deeper waters. A comparatively rare variation of this form is the twilight DVM, where the ascent occurs during the dusk and the descent around midnight, i.e. midnight sinking (Cushing, 1951). For herbivorous zooplankton, DVM is typically a strategy that allows feeding in the food-rich upper pelagial during the darker hours when light-dependent (visual) predation risk is minimal and to take refuge in the deeper waters during the daytime (Fig. 1) (Lampert, 1993). In contrast to the above classic patterns, reverse DVM (daytime ascent and night-time descent) likely enables zooplankton to evade light-independent (non-visual) invertebrate predators that perform classic DVM to escape their own visual predators (Fig. 2) (Ohman *et al.*, 1983).

(1) Control mechanisms

(*a*) Hypotheses about the proximate control of DVM

Until the mid-20th century, DVM studies were largely focused on understanding proximate control mechanisms (Fig. 3). Most proposed hypotheses reflected the tendency of zooplankton diel vertical behaviour to covary with irradiance (light) and temperature (reviewed in Russell, 1927; Forward 1988). It was thus suggested that zooplankton remain at depths during the daytime and migrate to near-surface waters during the night either in search of preferred levels or to avoid harmful levels of irradiance or temperature (Cuvier, 1817; Weismann, 1874; Parker, 1902; Russell, 1926; Clarke, 1934). Thermally stratified upper pelagial of lakes and the ocean may act as a barrier for some vertically migrating zooplankton, and consequently, many freshwater and marine zooplankton remain below the thermocline during daytime when the stratification is most pronounced (Russell, 1927; Cushing, 1951). Temperature can also induce changes in the irradiance sensitivity of some zooplankton, where animals that are negatively phototactic at lower ambient temperatures may become positively

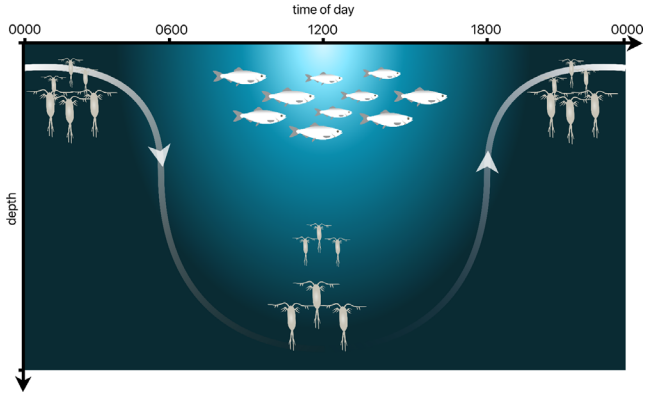

Fig 1. Unscaled conceptual model of classic (nocturnal) diel vertical migration based on Zaret & Suffern (1976). The upper pelagial is food rich but offers greater detection efficiency for visual predators (fish) during daytime. Copepods thus remain at depths during the day and ascend to the upper pelagial for feeding as the night approaches.

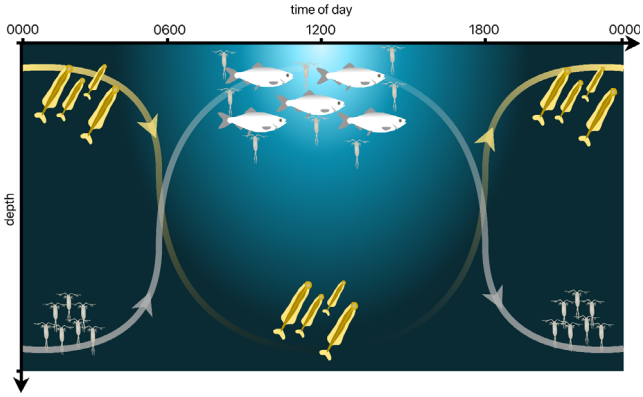

Fig 2. Unscaled conceptual model for reverse diel vertical migration based on Ohman *et al.* (1983). Visually feeding planktivores (fish) prefer larger prey and drive a classic DVM pattern (indicated in yellow) among larger zooplankton (chaetognaths). As smaller zooplankton (copepods) are predated upon by the chaetognaths and are less preferred by the visual predator, they perform a reverse DVM (indicated in grey).

phototactic at higher temperatures (Esterly, 1919). A temperature-induced change in the animal's phototactic reactions may alter the DVM behaviour if it is controlled by the ambient irradiance.

Relationships between DVM and irradiance were investigated in detail through myriad field and laboratory experiments conducted in the 20th century. Accordingly, the role of irradiance (in the spectral range 400–700 nm) in stimulating zooplankton DVM is described in three main hypotheses: the isolume hypothesis, absolute intensity hypothesis, and the rate-of-change hypothesis (Cohen & Forward, 2009). The oldest of the three, the isolume hypothesis (Ewald, 1910; Michael, 1911; Russell, 1927), suggests that zooplankton migrate up and down the water column in an attempt to maintain their vertical position according to an optimal or preferred range of light intensities. In the absolute light intensity hypothesis (Sweatt & Forward, 1985*a*,*b*), the ascent and descent reactions are triggered by a threshold irradiance level, thus producing an all-or-none DVM response. According to the rate-of-change hypothesis (Clarke, 1930; Ringelberg, 1964), changes in the relative rate and direction of irradiance are the proximate triggers of DVM. Empirical evidence supporting each of these hypotheses are paramount and are extensively reviewed in Forward (1976, 1988) and Ringelberg (1995*b*, 1999).

An observation that challenged the temperature- and irradiance-related hypotheses was mentioned by Brook (1886), who noted large daytime near-surface aggregates of the copepod *Calanus finmarchicus* in a Scottish loch (Loch Fyne) during the spring of 1885. At this time, the abundance of Atlantic herring (*Clupea harengus*) in the loch was extremely low, largely due to extensive daytime trawling. As the trawling ceased in summer, herring abundance increased and the daytime near-surface aggregations of

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

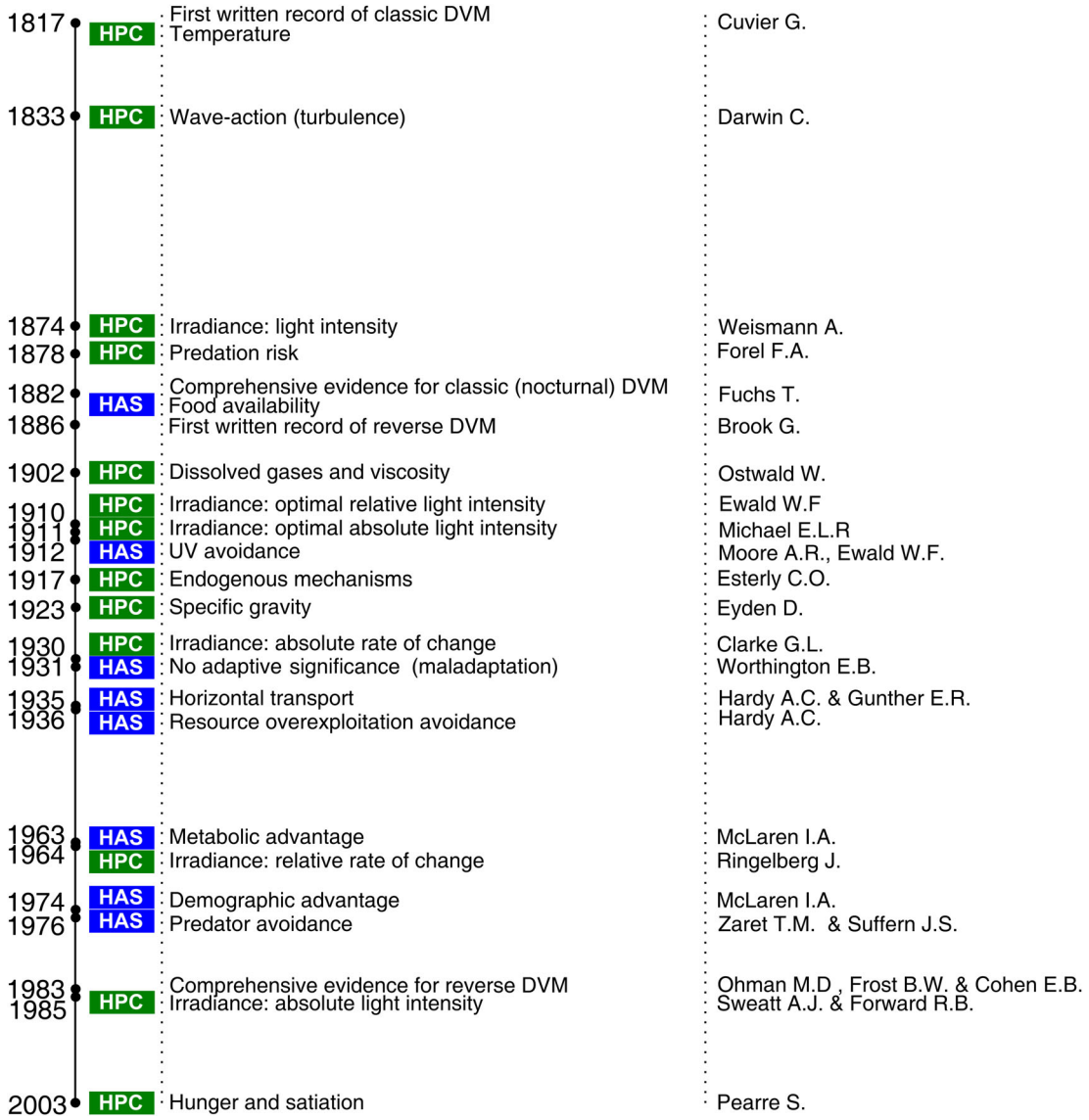

Fig 3. Development of main hypotheses about the proximate control (HPC) and adaptive significance (HAS) of zooplankton diel vertical migration (DVM).

C. finmarchicus rapidly decreased. This is possibly due to increased predation risk, especially since copepods comprised the main diet of Atlantic herring of Loch Fyne (Brook & Calderwood, 1885). Therefore, it is likely that the herbivorous copepod *C. finmarchicus* occupied the food-rich upper pelagial during daytime when herring predation was low irrespective of the higher temperatures and irradiance expected closer to the sea surface. Occupation of the upper pelagial during daytime and descending to deeper pelagial during the night is a reverse pattern of the classic DVM. Although several subsequent authors reported similar reverse migratory patterns among a number of zooplankton taxa (e.g. Herdman, 1907; Tattersall, 1911; Bayly, 1963; Bosch & Taylor, 1973), they did not receive much attention until the late 20th century, when Ohman *et al.* (1983) provided the first comprehensive empirical evidence to support reverse DVM. Observations of reverse DVM patterns not only highlighted the plasticity of zooplankton diel vertical behaviour but shed new light on the role of food availability and predation risk as potential control mechanisms.

The earliest insights about food- and predation-related proximate control of classic DVM date back to the late 19th century. These include the views of Forel (1878) that avoidance of sunlit waters by many pelagic crustaceans is due to the presence of pelagic fish, and Fuchs (1882) that DVM could be a feeding migration. However, these food- and predation-related hypotheses were not much tested at the time, possibly due to the extensive focus on temperature and irradiance as the main proximate cues of DVM. Today, numerous experimental and modelling studies demonstrate

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

how food availability can trigger, halt or modify zooplankton DVM (e.g. Huntley & Brooks, 1982; Pijanowska & Dawidowicz, 1987; Fiksen & Giske, 1995; Bandara *et al.*, 2018). Similarly, myriad studies highlight the ability of predation risk to modify DVM patterns through predator-induced mechanical disturbances (e.g. Bollens & Frost, 1989*a*; Bollens, Frost & Cordell, 1994) and chemical exudates (e.g. Loose & Dawidowicz, 1994; Reede & Ringelberg, 1995; Von Elert & Pohnert, 2000; Lass & Spaak, 2003; Beklioglu, Telli & Gozen, 2006).

Cues that stimulate DVM are not always exogenous (i.e. having an external cause or origin). Esterly (1917) observed persistent DVM behaviour in copepods kept under continuous darkness and hypothesised that DVM is regulated by an endogenous (i.e. having an internal cause or origin) mechanism. Ringelberg & Servaas (1971) investigated the previously reported circadian rhythm in the vertical migratory behaviour of *Daphnia magna* (Harris, 1963) and found that it shifted from 24 to 28 h when the daily light regime was altered from 12 h:12 h to 24 h:0 h (light: dark). The authors wrote: "*The persistence of the rhythm in what seems to be constant conditions and above all the phase shift demonstrates that the change in readiness to perform a phototactic reaction is endogenous*" (Ringelberg & Servaas, 1971, p. 291). Endogenous circadian rhythms (*circa* = approximately, *dies* = day) are not the only biological clocks through which zooplankton DVM is modulated. DVM and related swimming or metabolic activities sometimes co-oscillate with tidal cycles [circa-tidal rhythms of *ca.* 12.4-h periodicity (Cronin & Forward, 1979; Hill, 1991; Douglass, Wilson & Forward, 1992; Kimmerer, Buran & Bennett, 1998)], daily lunar cycle and monthly lunar phase [circa-lunar rhythms of *ca.* 24.8-h and 29.5-day periodicities (Alldredge & King, 1980; Gliwicz, 1986*a*; Benoit-Bird, Au & Wisdoma, 2009)]. For example, Last *et al.* (2016) reported a periodical shift of DVM from a 24-h circadian rhythm in the autumn to a 24.8-h circa-lunar rhythm during the winter in the high Arctic. Further, their acoustic observations showed a large-scale periodic sinking behaviour of pelagic zooplankton during the periods of full moon in synchrony with a 29.5-day lunar phase.

Although the molecular basis of the circadian rhythms of insects and mammals are extensively studied, those of zooplankton have only been investigated recently. In many plants and animals, a group of photoreceptor proteins called cryptochromes are responsible for the reception and signalling of UV-A and blue light (Lin & Todo, 2005). The amino acid sequence of cryptochromes is strikingly similar to photolyase enzymes, which play a central role in repairing UV-induced DNA damage. This led to the hypothesis that cryptochromes are evolutionary descendants of photolyases (Sancar, 2003). Since photolyases have a functional role interconnecting both DNA and irradiance, it is likely that DVM behaviour is synchronised to predictable diel oscillations of irradiance through cryptochrome-mediated changes in gene expression (Cashmore *et al.*, 1999; Gehring & Rosbash, 2003). Recent research on numerous freshwater and marine zooplankton taxa suggests that endogenous circadian clocks are mediated by the interactions of clock genes and their protein products that produce cyclic gene activity with diel periodicity (e.g. Tilden *et al.*, 2011; Biscontin *et al.*, 2017; Häfker *et al.*, 2017; Maas *et al.*, 2018; Hüppe *et al.*, 2020). However, endogenous circadian clocks are not entirely accurate and need to be entrained (calibrated) by exogenous cues, which appears to be irradiance in many species of invertebrates, vertebrates and plants (e.g. Giuliano *et al.*, 1988; Zeng *et al.*, 1996; Whitmore, Foulkes & Sassone-Corsi, 2000). Accordingly, DVM is likely a behaviour that is founded in genetic material, entrained and expressed with the aid of ambient irradiance (the primary exogenous cue), which may be modified by secondary factors such as temperature, food availability and predation risk (Gehring & Rosbash, 2003; Gaten *et al.*, 2008).

Apart from the main hypotheses discussed above, several alternative hypotheses on the proximate control of DVM exist. In his *Beagle* diary, Charles Darwin noted that the periodic retreat of zooplankton from near-surface waters was driven by the intense wave action on the sea surface (Darwin, 1833). Diel changes in salinity, density (e.g. Esterly, 1919; Eyden, 1923; Rudjakov, 1970) and dissolved gases (e.g. Ostwald, 1902) are also seen as proximate cues for DVM. In an extensive literature review, Pearre (2003) hypothesised that DVM may be driven by the state of hunger and satiation of individual zooplankton – hence the observed variability in the timing of migration among the individuals of a population (e.g. Pearre, 1979; Hays, Kennedy & Frost, 2001).

(*b*) Hypotheses about the adaptive significance of DVM

Initial insights into the adaptive significance of zooplankton DVM were made in the early 20th century (Fig. 3). Ewald (1912) and Moore (1912) discussed whether DVM is a behaviour that minimises the exposure of zooplankton to harmful UV radiation. According to Gehring & Rosbash (2003), zooplankton use their blue-light reception capability to perceive diel variation of irradiance and perform DVM to reduce UV-induced DNA damage. A comprehensive theoretical basis of the UV-avoidance hypothesis was recently formulated by Williamson *et al.* (2011), with a wealth of supporting evidence sourced from clear freshwater lakes (e.g. Rhode, Pawlowski & Tollrian, 2001; Wissel & Ramacharan, 2003; Alonso *et al.*, 2004; Mous, Van Densen & Machiels, 2004; Cooke *et al.*, 2008; Kessler *et al.*, 2008).

A different line of reasoning led Hardy & Gunther (1935) to suggest that migrating to deeper waters would allow zooplankton to drift with water currents to regions with better feeding opportunities. Empirical evidence supporting this hypothesis is common but comes mostly from estuarine systems (e.g. Bosch & Taylor, 1973; Kimmerer & McKinnon, 1987; Hill, 1991). Following his theoretical modelling work, McLaren (1963) suggested that feeding for part of the day in warmer, near-surface waters and occupying colder waters for the rest of the day is metabolically advantageous for zooplankton (see also Enright, 1977). In a different

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

perspective, McLaren (1974) posited that spending part of the day in deeper colder waters can result in increased zooplankton size at sexual maturity. Lower temperatures increase development times and thus allow longer time windows at each developmental stage for the organisms (invertebrates) to grow (Campbell *et al.*, 2001; Forster & Hirst, 2012; Maps, Pershing & Record, 2012*a*), producing relatively large females in the population with higher fecundity (Bandara *et al.*, 2019). Although these studies appear to be theoretically sound, empirical evidence suggests that these model predictions are not entirely accurate (Lock & McLaren, 1970; Orcutt & Porter, 1983; Reichwaldt & Stibor, 2005).

A weakness shared among the above hypotheses is their inability to provide a satisfactory explanation for reverse DVM. In the mid-20th century, ecologist George Evelyn Hutchinson addressed this weakness. In *A treatise on limnology*, Hutchinson (1967) revisited the earlier ideas of Forel (1878) and Fuchs (1882) and suggested that DVM of zooplankton is a behaviour that utilises feeding opportunities in near-surface waters when predation risk is minimal. Although several contemporary studies highlighted the trophic relationships between planktivorous fish and vertically migrating zooplankton (e.g. Beamish, 1966; Reif & Tappa, 1966; Narver, 1970), the observed DVM patterns were not interpreted in the light of predator avoidance. Hutchinson's synthesis strongly echoed in the work of Zaret & Suffern (1976), who provided the first comprehensive field evidence to support the predator-evasion hypothesis. Zaret & Suffern (1976) related the DVM behaviour of the pelagic copepod *Diaptomus gatunensis* to the efficiency of near-surface daytime feeding behaviour of the visually hunting planktivorous fish *Melaniris chugresi* in a tropical lake. As observations of the gut contents of the planktivore indicated a surprising lack of *D. gatunesis* in its diet (despite a preference for the latter), the authors argued that the daytime avoidance of near-surface waters by the copepod minimised the risk of being captured by *M. chugresi*. Zaret & Suffern (1976, p. 808) further wrote: "*our data strongly suggest that the vertical migration pattern of* D. gatunensis *in Gatun Lake is adaptive in that it reduces fish predation and that this pattern may have evolved as a response to predation pressures*". A wealth of evidence emerging from field and laboratory experiments (e.g. Gliwicz, 1986*b*; Dodson, 1990; Bollens & Frost, 1991; Lampert, 1993; Onsrud & Kaartvedt, 1998; Fortier *et al.*, 2001) and modelling studies (e.g. De Robertis, 2002; Thygesen & Patterson, 2018; Bandara *et al.*, 2019; Pinti & Visser, 2019) support the predator-evasion hypothesis.

(2) Plasticity of DVM

The predator-evasion hypothesis, which is based on light-dependent predation risk, does not consider the ability of predators to adjust their behavioural strategies in response to those of their prey. However, complex vertical habitat selection 'games' can emerge when both the predator and prey become vertical migrants, i.e. where the strategy followed by one actor, such as prey, impacts what is optimal for the predator, and *vice versa*. Game theory and the concept of evolutionarily stable strategies (ESS) have been central to evolutionary ecology (Maynard Smith, 1982) and zooplankton migrations and habitat choice have been modelled as games. Early efforts typically modelled two habitats (Iwasa, 1982; Gabriel & Thomas, 1988) whereas more recent efforts have extended this to a continuum of habitats (Pinti & Visser, 2019). Results from game models highlight the complex inherent dynamics of migrations as environmental conditions and properties of prey or predators change (Hugie & Dill, 1994; Pinti & Visser, 2019).

Reverse DVM is an excellent example of the plastic nature of zooplankton migrations. Ohman *et al.* (1983) observed a reverse DVM in smaller copepods of the genus *Pseudocalanus* and a concurrent classic DVM in several species of predatory copepods and chaetognaths in a temperate fjord (Dabob Bay, Puget Sound). Gut content analysis of the dominant fish species of the bay showed a strong preference towards larger predatory zooplankton and weaker preference towards the smaller *Pseudocalanus* spp. These findings led the authors to conclude that the classic DVM of larger zooplankton is a strategy to minimise fish encounters and the reverse DVM of smaller copepods is a strategy to minimise the spatial overlap with vertically migrating invertebrate predators. In fact, zooplankton DVMs may (*i*) transit from the classic variant to the reverse variant (daytime ascent and night-time descent), (*ii*) alter periodicity and amplitude, and (*iii*) sometimes completely cease depending on the vertical migratory behaviour of invertebrate (e.g. Levy, 1990; Neill, 1990; Frost & Bollens, 1992; Gilbert & Hampton, 2001; Tarling *et al.*, 2002; Irigoien, Conway & Harris, 2004) or vertebrate predators (e.g. Bollens & Frost, 1991; Sims *et al.*, 2005; Shepard *et al.*, 2006; Wilson *et al.*, 2006; Gleiss *et al.*, 2013; Hozumi *et al.*, 2018). In addition, the periodicity and amplitude of DVM can be plastic to a number of external environmental variables (Table 1) and shows extraordinary diversity among species and among individuals of the same species depending on their ontogeny, body size, colour, body condition and sex (e.g. Uye, Huang & Onbe, 1990; Hays *et al.*, 1994, 2001; Osgood & Frost, 1994; Sekino & Yamamura, 1999; De Robertis, Jaffe & Ohman, 2000; Pearre, 2003; Tarling, 2003; Sainmont *et al.*, 2014). For example, the ability to swim faster and efficiently over longer distances increases with developmental progression (as new swimming appendages emerge) and body size of zooplankton (Mauchline, 1998). Further, the size-dependent predation risk caused by visually searching predators also increases with the body size of the prey (zooplankton). Consequently, larger zooplankton in advanced developmental stages (e.g. late juveniles and adults) tend to perform frequent diel vertical excursions with greater amplitude compared to smaller bodied animals in earlier developmental stages (Hays, 1995; Ohman & Romagnan, 2016).

(3) Costs and risks of DVM

Herbivorous diel vertical migrants periodically abandon warmer, food-rich, near-surface waters and spend a part of the

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1. External environmental variables that may influence the periodicity and amplitude of diel vertical migration. The cited literature serves as examples and do not represent an exhaustive review

Environmental variable	References
Sunlight	Ewald (1910); Michael (1911); Russell (1927); Clarke (1930); Ringelberg (1964); Sweatt & Forward (1985*a*); Sweatt & Forward (1985*b*); Błachowiak-Samołyk *et al.* (2006); Cottier *et al.* (2006); van Haren & Compton (2013)
Moonlight	Alldredge & King (1980); Gliwicz (1986*a*); Webster *et al.* (2015); Last *et al.* (2016); Petrusevich *et al.* (2016)
Starlight and light from aurorae	Cohen & Forward (2002); Berge *et al.* (2009); Båtnes *et al.* (2015); Cohen *et al.* (2015)
Artificial sources of light	Moore *et al.* (2000); Davies *et al.* (2014); Ludvigsen *et al.* (2018)
Ultraviolet radiation	Speekmann, Bollens & Avent (2000); Leech & Williamson (2001); Rhode *et al.* (2001); Alonso *et al.* (2004); Wold & Norrbin (2004); Fischer *et al.* (2006); Cooke *et al.* (2008)
Bottom depth and water transparency	Dickson (1972); Gliwicz & Pijanowska (1988); Wissel & Ramacharan (2003); Mous *et al.* (2004); Kessler *et al.* (2008); Williamson *et al.* (2011); Tiberti & Iacobuzio (2013); Fischer *et al.* (2015); Leach *et al.* (2015); Aarflot *et al.* (2019)
Food availability	Isaacs, Tont & Wick (1974); Huntley & Brooks (1982); Johnsen & Jakobsen (1987); Pijanowska & Dawidowicz (1987); Andersen & Nival (1991); Dini & Carpenter (1992); Loose & Dawidowicz (1994); Fiksen & Giske (1995); Fiksen & Carlotti (1998); Van Gool & Ringelberg (1998); Tarling *et al.* (2000); Muluk & Beklioglu (2005); Beklioglu *et al.* (2008); Bandara *et al.* (2018)
Temperature	Calaban & Makarewicz (1982); Gerritsen (1982); Haney (1993); Loose & Dawidowicz (1994); Fiksen & Giske (1995); Williamson *et al.* (1996); Winder, Boersma & Spaak (2003); Muluk & Beklioglu (2005); Berge *et al.* (2014); Glaholt *et al.* (2016); Bandara *et al.* (2018)
Salinity	Lance (1962); Grindley (1964); Kimmerer *et al.* (1998); Coyle & Pinchuk (2005)
Dissolved oxygen	Longhurst (1967); Svetlichny *et al.* (2000); Hidalgo, Escribano & Morales (2005); Muluk & Beklioglu (2005); Bezerra-Neto & Pinto-Coelho (2007); Tremblay *et al.* (2010); Bianchi *et al.* (2013); Doubek *et al.* (2018)
Ice cover	Haney & Hall (1975); Fischer & Visbeck (1993); Saito & Hattori (1997); Brierley & Watkins (2000); Fortier *et al.* (2001); Cisewski *et al.* (2010); Wallace *et al.* (2010); Cohen *et al.* (2015); Cisewski & Strass (2016); Petrusevich *et al.* (2016)
Cloud cover, smoke and dust	Wold & Norrbin (2004); Kyba *et al.* (2011); Urmy *et al.* (2016)
Solar and lunar eclipses	Sherman & Honey (1970); Bright *et al.* (1972); Tont & Wick (1973); Kampa (1975); Tarling, Buchholz & Matthews (1999); Strömberg *et al.* (2002); Economou *et al.* (2008)
Diseases and parasites	Decaestecker, De Meester & Ebert (2002); Fels, Lee & Ebert (2004); Duffy *et al.* (2011); Johnson *et al.* (2018)

day in colder, usually food-limited deeper waters. This tends to reduce growth and development rates and induces fecundity losses (Stich & Lampert, 1984; Ohman, 1990; Dawidowicz & Loose, 1992*b*; Loose & Dawidowicz, 1994; Ringelberg & Van Gool, 2003; Bandara *et al.*, 2018). The energetic demands of swimming incur additional metabolic costs among diel vertical migrants, which is estimated to range between 0 and 300% of the basal metabolic rate (Petipa, 1966; Vlymen, 1970; Klyashtorin & Yarzhomb, 1973; Foulds & Roff, 1976; Morris, Gust & Torres, 1985; Alcaraz & Strickler, 1988; Dawidowicz & Loose, 1992*a*). However, given the difficulties of experimental manipulation and the number of internal (e.g. lipid and buoyancy, diversity of swimming patterns) and external (e.g. temperature, salinity, dissolved oxygen, predation) variables that influence zooplankton vertical movements, it is difficult to derive an accurate estimate of DVM-related metabolic demands. An accurate estimation of energetic demands of DVM should also include those of crossing sharp density gradients, as stratified water can act as a barrier that tends to entrap smaller zooplankton species and younger developmental stages (Wells, 1960; Madhupratap *et al.*, 1981; Marcogliese & Esch, 1992).

Diel vertical migrants face the risk of being horizontally transported (advected) from their home range (habitat) by surface or sub-surface water currents or tides (Cronin & Forward, 1979; Anderson & Stolzenbach, 1985; Kimmerer & McKinnon, 1987; Hill, 1991; Kimmerer *et al.*, 1998; Smith *et al.*, 2001; Carr *et al.*, 2008). The degree of risk induced by these lateral drifts depends on the timing and depth dynamics of the migration in relation to those of the tide or current, and the contrasting conditions encountered at the home range and the advected environment.

Microscale turbulences caused by diel migrants during swimming make them increasingly vulnerable to tactile predators that rely on hydrodynamic disturbances to detect prey (Greene, 1986). Consequently, vertically moving zooplankton become more conspicuous prey for predators, such as chaetognaths that lay in ambush (sit and wait) in the water column (Saito & Kiørboe, 2001). Apart from predation, diel migrants also have an increased probability of encountering pathogenic microorganisms that occupy different parts of the water column (Heuch, Parsons & Boxaspen, 1995; Grossart *et al.*, 2010).

(4) Community and ecosystem consequences of DVM

The abandoning of sunlit near-surface waters by diel migrating herbivorous zooplankton allows a time window (daytime in the case of classic DVM) of low grazing pressure and high growth potential for phytoplankton populations

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(Bowers, 1979; Lampert & Taylor, 1985; Lampert, 1987). In his group selection discussions, Hardy (1936) mentioned the DVM of herbivorous zooplankton as a phenomenon that prevents overexploitation of pelagic primary production. However, DVM cannot have evolved to prevent resource overexploitation, as this would not be an evolutionarily stable strategy that would prevent the spread of cheating strategies (e.g. feeding at daytime, when competition is low) in the population (Maynard Smith 1979). Rather, the positive correlation observed between phytoplankton growth and DVM intensity in mathematical models (e.g. McAllister, 1969; Petipa & Makarova, 1969; Petzoldt *et al.*, 2009), laboratory experiments (Reichwaldt, Wolf & Stibor, 2004; Haupt *et al.*, 2009) and field studies (Reichwaldt & Stibor, 2005) appears to be simply a consequence of DVM.

DVM behaviour is not confined to zooplankton but is observed in various pelagic species of both lower and higher trophic levels. Laboratory experiments by Latta, O'Donnell & Pfrender (2009) and Bollens, Quenette & Rollwagen-Bollens (2012) demonstrated how DVM of several autotrophic flagellates could be top-down driven by zooplankton grazers. Such top-down-regulated migrations are referred to as 'cascading vertical migrations' (Bollens *et al.*, 2010). However, diel migratory patterns of adjacent trophic levels are not always regulated top-down. For example, DVMs of many visually feeding zooplanktivorous fish and mega-planktivores, such as ocean sunfish, filter-feeding sharks and baleen whales are commonly seen as diel prey-following behaviours (Table 2). Similarly, DVM of a variety of higher-level pelagic predators, such as mesopelagic fish and sharks, toothed whales, dolphins and seals are usually explained in the light of diel vertical behavioural patterns of their prey, often consisting of squids and various mid-trophic-level fish (Table 2). Therefore, contrasting and complex selection pressures seem to underlie the adaptive significance of DVM patterns observed along pelagic food webs. While the DVM of primary producers (flagellates) and primary consumers (herbivorous zooplankton) appear to be driven by predation risk, that of higher-order consumers is likely driven by spatio-temporal dynamics of food (prey) availability (Table 2). However, with the exception of a few model predictions (e.g. Thygesen & Patterson, 2018), there is little empirical evidence for trophic links between the observed DVM patterns of pelagic top predators and those of zooplankton. Therefore, it seems unlikely that the taxonomically widespread phenomenon of DVM is entirely a cascading top-down effect of trophic interactions.

Zooplankton play a central role in the ocean's biologically driven carbon sequestration process, which involves a downward flux of carbon from the atmosphere through deeper waters into the sediment ['biological pump' (Longhurst & Glen Harrison, 1989; Ducklow, Steinberg & Buessler, 2001; Hain, Sigman & Haug, 2014)]. Apart from feeding in near-surface waters and production of sinking faecal pellets (which are greater in density compared to dead phytoplankton and thus have a greater chance of reaching the seafloor), DVM adds a dynamic component to the biological pump because zooplankton tend to respire and defecate at greater depths (usually in the aphotic zone) during part of the day. The magnitude of the DVM-induced flux of organic matter depends on the species composition and biomass of zooplankton communities and is estimated to account for 4–70% of the total particulate organic carbon flux (reviewed in Ducklow *et al.*, 2001). However, the influence of cascading DVMs on the biological carbon sequestration process is not well understood and may add significantly to present estimates (Bollens *et al.*, 2010; Brierley, 2014).

Synchronised vertical movements of zooplankton can have a significant impact on the fluid motion and vertical water column structure at smaller spatial scales (Prairie *et al.*, 2012). Several studies have shown that macroplankton, micronekton and large groups of mesozooplankton can cause considerable turbulence during their diel vertical excursions. For example, Kunze *et al.* (2006) used a microstructure profiler to detect turbulence generated by a dense krill aggregate (densities $>10^4$ individuals m^{-3}) ascending to near-surface waters at dusk. They measured relatively high turbulence levels (10^{-5}–10^{-4} W kg^{-1}) in the upper pelagial for a short period of time during the peak ascent. They wrote: "*These values are 100 to 1000 times the dissipation rates associated with turbulence patches in the stratified deep ocean and are comparable to values found in strongly turbulent tidal channels*" (Kunze *et al.*, 2006, p. 1769). According to Katija & Dabiri (2009) vertically migrating jellyfish can transport fluids that adhere to their bodies across the water column (fluid drift), with possible implications for translocating nutrients and other particulate matter across density gradients. As zooplankton vertical migrations are followed by higher-order consumers, they produce a significant amount of turbulent kinetic energy, estimated to be *ca.* 4.5×10^{11} W throughout the world's oceans (Dewar *et al.*, 2006).

III. SEASONAL VERTICAL MIGRATION OF ZOOPLANKTON

Combining his own observations with those of Georg Ossian Sars, Peter Erasmus Müller and Anton Frič, the German biologist August Weismann summarised the ability of lacustrine daphnids to evacuate the pelagial seasonally and occupy the sediment as resting eggs (Weismann, 1876). Although this phenomenon was unknown in the marine realm at the time, Schmidtlein (1879) noted the tendency of some marine crustaceans to disappear from the upper pelagial in the summer–autumn months and reappear in the following spring. To investigate this further, Chun (1888) used depth-stratified net samples in the Mediterranean Sea and showed that the seasonal disappearance of jellyfish and crustaceans from the upper pelagial was due to their migration to depths below 1000 m. By the early 20th century, scientists started to use the term 'seasonal vertical migration' (SVM) to refer to this behaviour. Although not as widespread as DVM, SVM is a behavioural strategy common among many planktonic

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 2. Trophic-linked diel vertical migrations observed among pelagic communities. Migrations of motile primary producers (flagellates) and primary consumers (zooplankton) are largely viewed as predator-evasion strategies. Migrations of higher-order consumers (fish, cetaceans and diving birds) are largely viewed as prey-following strategies. The cited literature serves as examples and do not represent an exhaustive review

Trophic link	Migration undertaken by	Migration driven by	Primary selection pressure	References
PP–PC	Photosynthetic flagellates *Akashiwo sanguinea* *Chlamydomonas reinhardtii*	Herbivorous zooplankton *Acartia* spp. *Daphnia* spp.	Top-down	Latta *et al.* (2009); Bollens *et al.* (2012)
PC–SC	Herbivorous zooplankton *Daphnia* spp. *Bosmina* spp. *Diaptomus* spp. *Moina* spp. *Cyclops* spp. *Acartia* spp. *Pseudocalanus* spp. *Calanus* spp. *Meganyctiphanes norvegica*	Carnivorous zooplankton *Parasagitta* spp. *Themisto* spp. Zooplanktivorous fish *Clupea harengus* (Atlantic herring) *Osmerus mordax* (rainbow smelt) *Melaniris chagresi* (chagres silverside) *Gasterosteus aculeatus* (three-spined stickleback) *Leucaspius delineates* (sunbleak) *Boreogardus saida* (polar cod) *Perca fluviatilis* (European perch)	Top-down	Brook (1886); Reif & Tappa (1966); Zaret & Suffern (1976); Gliwicz (1986*b*); Bollens & Frost (1989*b*); Bollens & Frost (1991); Lampert (1993); Bollens *et al.* (1994); Loose & Dawidowicz (1994); Reede & Ringelberg (1995); Hays, Warner & Lefevre (1996); Onsrud & Kaartvedt (1998); Fortier *et al.* (2001); Picapedra, Lansac-Tôha & Bialetzki (2015)
	Visual feeding and filter feeding planktivores *Alosa pseudoharengus* (alewife) *Mola mola* (ocean sunfish) *Rhincodon typus* (whale shark) *Cetrohinus maximus* (basking shark) *Megachasma pelagios* (megamouth shark) *Eubalaena glacialis* (North Atlantic right whale) *Balaenoptera borealis* (sei whale)	Herbivorous zooplankton Copepods (e.g. *Calanus* spp.) Krill (*Meganyctiphanes norvegica*, *Thysanoessa* spp.)	Bottom-up	Winn *et al.* (1995); Nelson *et al.* (1997); Cartamil & Lowe (2004); Sims *et al.* (2005); Shepard *et al.* (2006); Wilson *et al.* (2006); Baumgartner & Fratantoni (2008); Baumgartner *et al.* (2011); Gleiss *et al.* (2013); Ishii *et al.* (2017); Hozumi *et al.* (2018)
SC–TC SC–QC	Pelagic top predators *Thunnus thynnus* (Atlantic bluefin tuna) *T. obesus* (bigeye tuna) *Xiphias gladius* (swordfish) *Coryphaena hippurus* (dolphinfish) *Alopias superciliosus* (bigeye thresher shark) *A. vulpinus* (common thresher shark) *Galeorhinus galeus* (school shark) *Prionace glauca* (blue shark) *Lamna ditropis* (salmon shark)	Mid-trophic-level fish and cephalopods	Bottom-up	Carey & Robinson (1981); Horning & Trillmich (1999); Dagorn, Bach & Josse (2000); Baird *et al.* (2001); West & Stevens (2001); Robin *et al.* (2002); Musyl *et al.* (2003); Born *et al.* (2004); Weng & Block (2004); Baird, Hanson & Dill (2005); Block *et al.* (2005); Aoki *et al.* (2007); Campana *et al.* (2011); Merten *et al.* (2014); Coffey *et al.* (2017); Heard *et al.* (2018)

(Continues)

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 2. *(Cont.)*

Trophic link	Migration undertaken by	Migration driven by	Primary selection pressure	References
	Physeter macrocephalus (sperm whale) *Globicephala melas* (pilot whale) *Orcinus orca* (killer whale) *Stenella attenuate* (pantropical spotted dolphin) *Arctocephalus* sp. (fur seals)			
TC–QC	*Mesoplodon densirostris* (Blainville's beaked whale)	*Orcinus orca* (killer whale)	Top-down	Baird *et al.* (2008)

PP, primary producers; PC, primary consumers; SC, secondary consumers; TC, tertiary consumers; QC, quaternary consumers.

inhabitants of seasonal environments (Conover, 1988; Hagen & Auel, 2001; Teuber *et al.*, 2019).

Some aquatic environments are characterised by predictable degradation of habitat quality in the (upper) pelagial during part of the year. In high-latitude environments and coastal upwelling systems, this occurs through seasonal depletion of primary production due to light or nutrient limitation. In many small freshwater systems (e.g. ponds and small lakes), summertime droughts often lead to seasonal temperature extremes in the pelagial and totally dry off under severe circumstances. Irrespective of the latitude, most pelagic environments exhibit seasonal oscillations of predation pressure. Consequently, life in the upper pelagial may become challenging for planktonic inhabitants during summer, due to harmful temperatures, droughts and predation risk, or in winter, due to freezing and loss of primary production (Clarke, 1988; Conover & Siferd, 1993; Hagen & Auel, 2001). As the conditions in these near-surface waters deteriorate, zooplankton descend (passively sink or actively swim down) to deeper waters or to the sediment and may enter a state of inactivity and suppressed development termed 'dormancy' (reviewed in Andrewartha, 1952; Vegis, 1964; Danks, 1987). When favourable environmental conditions return, dormancy terminates, and zooplankton ascend back to the upper pelagial. This periodic seasonal movement in and out of the upper pelagial characterises the SVM.

To date, there is no widely received definition for zooplankton SVMs. Zooplankton SVMs typically refer to extensive vertical movements, such as those with hundreds or thousands of metres of amplitude in the open ocean (e.g. Østvedt, 1955; Auel, Klages & Werner, 2003; Slagstad & Tande, 2007). Relatively shallow (low-amplitude) seasonal migrations also occur in many shallow coastal and freshwater bodies (Bagøien, Kaartvedt & Øverås, 2000; Cáceres & Tessier, 2004; Bandara *et al.*, 2016). In freshwater systems, these shallow vertical movements are seldom referred to as SVMs, possibly due to their trivial amplitudes compared to those in the open ocean. However, in this synthesis, we use the term SVM to denote a broad range of zooplankton seasonal vertical movements irrespective of the habitat and amplitude. This allows us to describe an array of interesting vertical habitat selection strategies related to dormancy of many marine and freshwater zooplankton in the light of SVM. In this regard, we refer to the Dahms (1995) definition and classification of zooplankton dormancy. Accordingly, dormancy is a state of suppressed development, which can either represent a relatively short episode of developmental retardation that occurs in response to a limiting factor in the environment, termed 'quiescence' or a long-lasting period of arrested development cued by predictable and cyclic environmental changes with an underlying genetic regulation, termed 'diapause' (see also Danks, 1987). Based on different diapause strategies of zooplankton, SVM can be classified into: (*i*) low-amplitude (depth) SVM of resting stages that undergo diapause in or on the sediment, and (*ii*) high-amplitude SVM of late-juvenile and adult stages that 'overwinter' or 'oversummer' in the deeper pelagial.

(1) Low-amplitude SVM of resting stages

The production of resting stages is largely limited to freshwater zooplankton occupying shallow ponds, rivers and lakes, and marine zooplankton inhabiting coastal waters (reviewed in Uye, 1985; Marcus, 1996; Gyllström & Hansson, 2004). The SVM amplitude of resting-stage-producing zooplankton thus ranges from a few centimetres to several metres in most freshwater habitats (Wood, 1932; Garcia-Roger, Carmona & Serra, 2006) and seldom exceeds 100 m in the ocean (Lindley, 1990; Engel & Hirche, 2004). Zooplankton can enter diapause as either embryonic or non-embryonic resting stages.

(*a*) SVM of embryonic resting stages

Wintertime developmental suppression and the production of dormant embryos of freshwater cladocerans have been studied since the early 18th century (Fryer, 1996). For

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

example, Cuvier (1817, p. 342) combined his own observations and those of Straus Durkheim and Claude Schaeffer on dormant embryos of *Daphnia* and wrote: "…*each capsule encloses an egg, with a horny and greenish shell, similar in other respects to the common eggs, but remaining longer without being developed, and passing the winter under this form*". By the late 19th century, the term 'resting eggs' was widely used to represent these dormant embryonic stages (e.g. Weismann, 1876; Forel, 1882). Numerous freshwater and marine zooplankton, including rotifers, cladocerans and copepods produce resting eggs (reviewed in Grice & Marcus, 1981; Pourriot & Snell, 1983; Onbé, 1991). For example, in small barnyard ponds, females of the freshwater cladoceran *Moina macrocopa* switch from a parthenogenetic reproductive mode to a gametogenic mode when the water level drops and the pond becomes increasingly crowded in summer (Wood, 1932; Zadereev, 2003). Following gametogenesis, each female produces about two resting eggs, which are deposited in a special egg case called the ephippium (Grosvenor & Smith, 1913; Cheng, 1947). Resting eggs are usually larger than parthenogenetic (subitaneous) eggs, rich in lipid droplets and have a thicker chorion that protects against desiccation, predation and bacterial degradation (Dahms, 1995; Strachan, Chester & Robson, 2015). Once fertilization occurs, the egg case is released into the water and sinks to the sediment, where they may remain in a state of diapause for several months. During diapause, resting eggs often can sustain harsh conditions of summertime droughts and wintertime freezing and hatch when the pond refills with rainwater in the following spring (Wood, 1932). Newly hatched instars return to the pelagial and develop into adults, thus completing the life cycle (Fig. 4).

(*b*) SVM of non-embryonic resting stages

Some zooplankton can enter diapause in their late-juvenile or adult stages that descend to the sediment in shallow aquatic habitats. In rotifers and copepods, these resting stages are sometimes encysted in a cuticulin housing that facilitates sinking and provides protection from predation and desiccation (reviewed in Dahms, 1995; Ricci, 2001; Radzikowski, 2013). If the encystment of the developmental stages occurs in the pelagial, they sink passively and settle on the sediment (Baumgartner & Tarrant, 2017). Late-juvenile or adult developmental stages of some zooplankton species swim actively into the sediment, within which their encystment occurs (Gyllström & Hansson, 2004). In many other species, resting stages remain non-encysted during diapause (Fryer & Smyly, 1954; Elgmork, 1962; Sarvala, 1979). For example, Næss & Nilssen (1991) documented non-encysted diapausing adults of the freshwater copepod *Cyclops strenuus* from the sediments of a *ca.* 20 m-deep lake in southern Norway. *C. strenuus* occupies the upper pelagial during spring and summer and develop into sexually mature adults (see also Elgmork, 1955, 1959). Although females are fertilised in autumn, their egg production does not start until the following year. Instead, lipid-rich adult females store sperm in their spermathecae, swim down to the sediment and enter diapause. Females (together with viable sperm) remain in diapause for *ca.* 6 months until their subsequent emergence and seasonal ascent to the upper pelagial in late winter (see also Bruno *et al.*, 2001). As the stored sperm are released and eggs are fertilised, the production of the new generation of *C. strenuus* occurs in early spring in the absence of adult males, who do not undergo diapause (Fig. 5). The occurrence of diapausing fertilised females and the ensuing early reproduction are thus seen as adaptive strategies to avoid intense competition for food and minimise mortality risk that usually peak in late spring and summer (Næss & Nilssen, 1991).

(2) High-amplitude SVM of overwintering and oversummering stages

High-amplitude vertical migrations are typically undertaken by late-juvenile or adult stages that swim down to greater depths in response to or preceding seasonal deteriorations of the environment that occur in the upper pelagial during winter (overwintering; Sømme, 1934) or summer (oversummering; Wang, Zuo & Wang, 2003). Since the observations of oversummering are comparatively rare, this synthesis will primarily focus on SVM patterns related to overwintering strategies of zooplankton.

Overwintering is not an exclusively marine phenomenon, but is common among several species of freshwater cladocerans and copepods occupying relatively deep, seasonally ice-covered lakes (e.g. Elgmork, 1959; Hall, 1964; Santer *et al.*, 2000; Schneider *et al.*, 2016). In freshwater literature, overwintering is often referred to as 'active diapause' (Wolcott, 1934) because the metabolic activity of overwintering stages is relatively high compared to resting eggs (Hand, 1991). Reviewing vertical distribution data of numerous temperate freshwater lakes, de Senerpont Domis *et al.* (2007) found a shift in *Daphnia* spp. diapause strategy from resting egg production in shallower lakes to overwintering in deeper lakes. Similarly, in the marine realm, resting egg production is more common among zooplankton occupying shallow coastal habitats (Marcus, 1996). Therefore, overwintering appears to be a more successful strategy in deep marine environments, possibly driven by the decreased viability of resting eggs at greater depths. For example, a resting egg released closer to the surface in a several hundred metres deep water column has a high probability of being predated prior to reaching the bottom (see also Brendonck & De Meester, 2003). Further, unless assisted by upwelling currents and positive buoyancy, it is less likely for the newly hatched instars to ascend to the upper pelagial in the following spring, given their slow swimming speeds and greater migration depths (Mauchline, 1998).

In the marine realm, SVM and overwintering strategies are documented across various latitudes extending from the tropics to polar regions (Record *et al.*, 2018; Kvile, Ashjian & Ji, 2019). While the classic SVM and overwintering observations are generally made in high-latitude systems, similar observations are not uncommon at lower

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

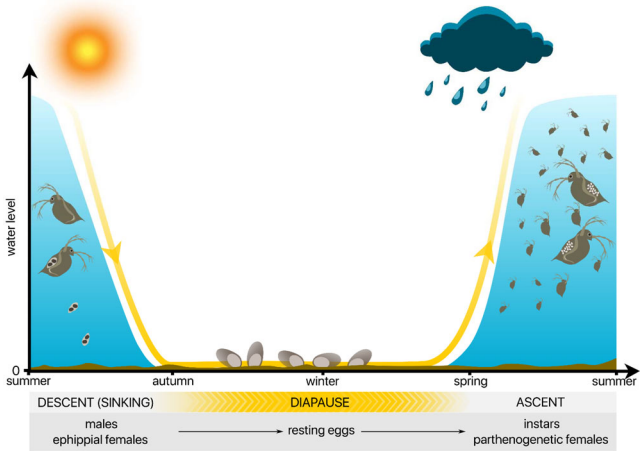

Fig 4. Unscaled conceptual model for summer diapause and low-amplitude seasonal vertical migration of a pond-dwelling cladoceran based on Wood (1932). As the shallow pond gradually dries out due to extensive evaporation during summer, male and female encounter rates increase, and sexual reproduction begins. This results in the production of resting eggs (ephippia), which are cast to the sediment and undergo diapause. Resting eggs hatch when rain refills the pond in the following spring. Until next summer, the animals reproduce asexually by parthenogenesis. Diel environmental and behavioural dynamics are not presented.

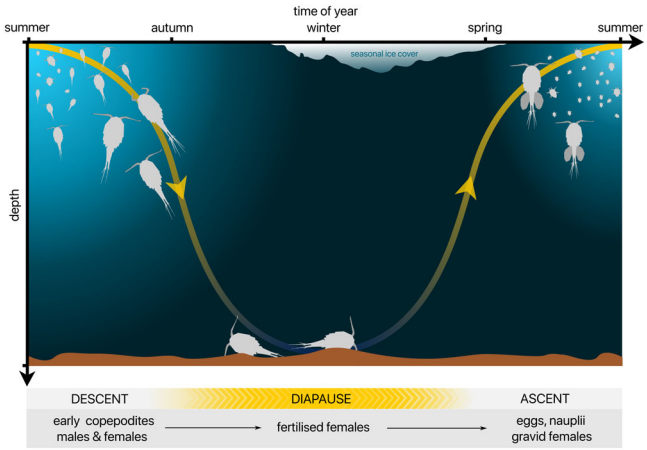

Fig 5. Unscaled conceptual model for winter diapause and seasonal vertical migration of a high-latitude lacustrine cyclopoid copepod based on Næss & Nilssen (1991). Animals feed in the upper pelagial during the relatively short productive season and sexually reproduce in autumn. Although no eggs are produced, females store the sperm and swim down to the sediment for diapause. Diapause terminates at the onset of the following productive season and fertilised females ascend to shallower waters to produce eggs. Diel environmental and behavioural dynamics are not presented.

latitudes, where the seasonality is driven mainly by periodic upwelling events.

(*a*) SVM in high-latitude environments

In Arctic and Antarctic settings where the productive season is typically short, herbivorous copepods in the genera *Calanoides*, *Eucalanus*, *Calanus* and *Neocalanus* are well known to perform SVM (Longhurst, Sameoto & Herman, 1984; Miller *et al.*, 1984; Schnack-Schiel & Hagen, 1994; Atkinson, 1998; Gislason, 2018). Younger developmental stages of these copepods often thrive in warmer, food-rich, near-surface waters, and grow and develop rapidly during the productive season (spring and summer) (Conover, 1988; Schnack-Schiel, 2001; Varpe, 2012). Seasonal changes of irradiance, nutrient limitation and grazing pressure tend to limit the pelagic primary production during late summer and autumn (Lalli & Parsons, 1993; Sakshaug *et al.*, 2009). Consequently, the growth and development of species with relatively larger body size (e.g. *Calanus glacialis*, *C. hyperboreus*) become time-constrained, and consequently, they cannot usually complete the life cycle within a single productive season. Although species with smaller body size (e.g. *C. finmarchicus*, *Eucalanus bungii*) may complete several generations within a single productive season (Tsuda, Saito & Kasai, 2004; Melle *et al.*, 2014), overwintering becomes inevitable as the food supply fades towards autumn. Older developmental stages of these copepods (e.g. copepodite stages III, IV and V) migrate to deeper waters with accumulated lipid reserves for overwintering (Lee, 1975; Hagen & Auel, 2001; Falk-Petersen *et al.*, 2009). These overwintering stages remain in deeper waters with limited physical and physiological activity (reviewed in Hirche, 1996*a*) and ascend back to the near-surface waters and complete their life cycle at the onset of the following productive season (Fig. 6).

Some high-latitude herbivorous copepods start their seasonal descent relatively early in the season, sometimes well before the termination of pelagic primary production (Schnack-Schiel, Hagen & Mizdalski, 1991; Kaartvedt, 2000). The actual cues that the copepods use to predict the termination of pelagic primary production and descend to overwintering habitats before the habitat quality deteriorates in the upper pelagial are not well known, but among the candidates are external cues, such as photoperiod (Sømme, 1934; Fiksen, 2000) or internal cues related to developmental stage and reserve levels (Johnson *et al.*, 2008). Further, factors other than food depletion, such as the summertime increase of temperature (Pu *et al.*, 2004), irradiance intensity (Russell, 1926) and predation risk (Kaartvedt, 2000; Varpe & Fiksen, 2010) may also be important drivers of these earlier seasonal descents. SVM patterns characterised by a summertime seasonal descent and an autumn–winter seasonal ascent are underlined by oversummering strategies. Oversummering has been documented for the temperate copepod *Calanus sinicus* in the Yellow Sea (Wang *et al.*, 2003; Li *et al.*, 2004) and the high-latitude copepod *C. finmarchicus* in the Gulf of Maine (Durbin *et al.*, 1997; Saumweber & Durbin, 2006; Maps *et al.*, 2012*b*).

SVMs are often observed among high-latitude carnivorous zooplankton, such as jellyfish, euphausiids and chaetognaths, and are generally seen as tracking the vertical trajectories of their herbivorous prey through the water column

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(David, 1958; Siferd & Conover, 1992; Torres *et al.*, 1994*a*; Bagøien *et al.*, 2000; Bandara *et al.*, 2016). Compared to their herbivore and carnivore counterparts, SVMs of high-latitude omnivorous zooplankton seem to be less pronounced, and this is viewed in the light of a year-round food supply (e.g. Metz, 1995; Richter, 1995; Falkenhaug, Taude & Semenova, 1997; Lischka & Hagen, 2005; Darnis & Fortier, 2014).

(*b*) SVM in upwelling environments

Oligotrophic waters of tropical and sub-tropical coastal regions become seasonally productive during the upwelling period, which is characterised by low temperatures and strong advection of water masses through Ekman transport (Barber & Smith, 1981; Brink, 1983). Numerous zooplankton taxa, including copepods, euphausiids and larval stages of various other crustaceans perform SVMs in these environments (e.g. Makarov, 1979; Pillar, Armstrong & Hutchings, 1989; Auel & Verheye, 2007; Morgan & Fisher, 2010). For example, in the Oregon and southern California Current upwelling systems, the older developmental stages (copepodite stages IV and V) of the herbivorous copepods *Calanus marshalle* and *C. pacificus* overwinter in deeper waters 25–50 km off the continental shelf (Peterson *et al.*, 1979; Wroblewski, 1982; Alldredge *et al.*, 1984). Physical activity of part of the overwintering population commences before the onset of the upwelling season, and they ascend to shoreward-moving downwelling currents, within which moulting to adult stages occurs (Peterson, 1998). As the physical activity of the other individuals commences in synchrony with the upwelling season, they ride upwelling currents to ascend shoreward and moult to adults (Peterson *et al.*, 1979). The reproduction of the newly moulted adults occurs within shallow, highly productive near-shore waters. This strategy allows *C. marshalle* and *C. pacificus* to produce several generations during the productive season before being eventually advected offshore, where they overwinter at depth as lipid-rich older developmental stages (Peterson, 1998) (Fig. 7).

The unproductive season of some tropical coastal upwelling systems can often extend over 10 months of the year (Demarcq, 2009; Hutchings *et al.*, 2009). For example, in the northern Benguela upwelling system, the productive upwelling season lasts for only a few months, and some zooplankton, such as the copepod *Calanoides carinatus* overwinter for up to 8–10 months of the year (Verheye, Hutchings & Peterson, 1991; Timonin *et al.*, 1992). To survive such prolonged overwintering periods at relatively high temperatures (6–8°C), *C. carinatus* reduces its wintertime metabolic rate by *ca.* 96% (Auel & Verheye, 2007). In comparison, high-latitude copepods occupying relatively colder waters (<4°C) only require an *ca.* 75% decrease of metabolic rate to survive a typically 6–8 month-long overwintering period (Maps, Record & Pershing, 2013).

SVM patterns in coastal upwelling regions have also been reported for carnivorous zooplankton and micronekton (e.g. Gorbunova, Evseenko & Garetovsky, 1985; Gibbons & Stuart, 1994; Rodríguez *et al.*, 2015). Similar to those observed among their high-latitude counterparts, these SVMs most likely represent seasonal prey-following strategies (see Fortier & Harris, 1989; Aita, Yamanaka & Kishi, 2003).

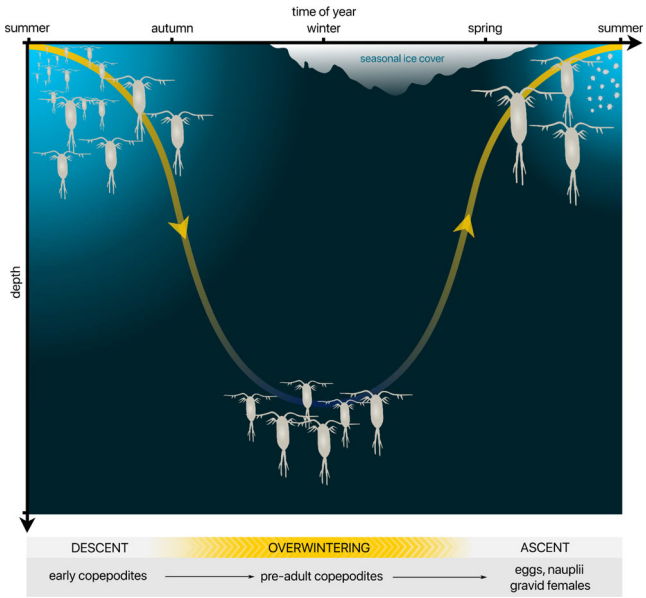

Fig 6. Unscaled conceptual model for seasonal vertical migration and overwintering of a high-latitude marine calanoid copepod based on Conover (1988). Animals feed in the upper pelagial during the short productive season (spring–summer) and late-juvenile (pre-adult) stages with accumulated lipid stores descend to overwintering depths on or before the termination of primary production (autumn–winter). The spring ascent occurs on or before the commencement of the following productive season, which is followed by moulting to adults, sexual reproduction and spawning. Diel environmental and behavioural dynamics are not presented.

(3) Control mechanisms

(*a*) Hypotheses about the proximate control of SVM

Compared to DVM, zooplankton SVMs operate on broader spatial (vertical) and temporal scales. Consequently, proximate control hypotheses focus on three main aspects of the migration, including the seasonal descent, seasonal ascent and the migration amplitude (i.e. vertical habitat selection). For most zooplankton (especially herbivores), the seasonal descent and ascent are either preceded or followed by a period of diapause. Due to this, any internal or external cues that induce or terminate diapause can be generally regarded as a cue for SVM (Fig. 8).

(i) Hypotheses about seasonal descent and diapause induction. Although the seasonal pelagic to benthic descent of lacustrine daphnids was well studied in the 19th century, the broad species- and location-specific variability of the timing of these migrations hindered drawing strong conclusions about the underlying proximate cues (Weismann, 1876;

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Forel, 1882; Frič & Vávra, 1897). Chun (1888) was probably the first to suggest that the seasonal descent of many species of marine jellyfish and crustaceans is likely due to their inability to tolerate higher summertime temperatures in the upper pelagial. Gran (1902) doubted whether the deep overwintering migrations of the copepods *Calanus finmarchicus* and *C. hyperboreus* in the Norwegian Sea is due to the seasonal depletion of phytoplankton in the upper pelagial. Birge (1904) observed a non-seasonally migrating population of the freshwater cladoceran *Daphnia longiremis* and suggested that it may underpin the year-round food availability in their lacustrine habitat. Birge (1904) also noted a seasonally migrating population of another daphnid (*D. pulicaria*), which occupied near-surface waters in spring and descended to deeper waters as summer approached. Birge suggested that the evacuation of near-surface waters may reflect the inability of *D. pulicaria* to tolerate elevated summertime irradiance. A similar observation was made in the marine realm by Russell (1926). He investigated the seasonal vertical distribution of the high-latitude copepod *C. finmarchicus* and suggested that its gradual summer–autumn descent is an adaptation to occupy depths with a preferred light intensity. Russell (1926, p. 427) wrote: "*we see then that if an animal is to be adapted to a certain light intensity, we should expect it to show variations in depth throughout the year, and that it should be at its deepest at mid-day on a sunny day in the middle of June*".

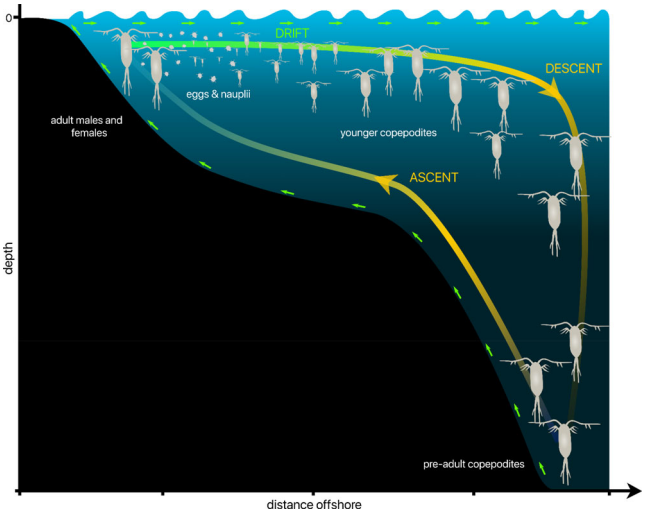

Fig 7. Unscaled conceptual model for seasonal ontogenetic vertical migration of a calanoid copepod in a coastal upwelling region based on Peterson (1998). Lipid-rich late-juvenile (pre-adult) stages overwinter off the shelf during the unproductive season. The overwintering period typically ends at the onset of the short productive season, and the copepodites ascend to rising upwelling currents, moult into adults and reproduce. Eggs are laid near the surface, and younger generation(s) develop in nearshore productive waters while drifting offshore over time. At the end of the productive season, copepodites descend to deeper waters for overwintering. The general direction of the water current is marked with green arrows. Diel environmental and behavioural dynamics are not presented.

The best-known hypotheses for diapause induction and seasonal descent of freshwater zooplankton involve temperature (e.g. Bhajan & Hynes, 1972; Hairston & Olds, 1986; Bernot *et al.*, 2006) irradiance (e.g. Gilbert, 1963; Kuo-Cheng Shan, 1974; Pasternak & Arashkevich, 1999) and food limitation (e.g. Scharfenberg, 1910; D'Abramo, 1980; Hansen & Hairston, 1998; Drillet, Hansen & Kiørboe, 2011) as proximate cues. However, given the typically large vertical extent (amplitude) of the migration, it is inexpedient to view most marine SVMs as a behaviour to avoid harmful irradiance or temperature (see also Banse, 1964; Marshall & Orr, 1972). For instance, neither Chun's temperature hypothesis (Chun, 1888) nor Russell's irradiance hypothesis (Russell, 1926) explain why the upper pelagial residents often descend several thousands of metres to take refuge from harmful temperature or irradiance when the waters below a few hundred metres are typically within a tolerable range.

Proximate control hypotheses based on cues of biological origin began to emerge in the early 20th century. The oldest of these is the induction of diapause among freshwater zooplankton in response to crowding (Grosvenor & Smith, 1913). In species whose resting eggs are sexually produced, crowding increases the chances of female and male encounters and thus elevates the production of resting eggs (Wood, 1932). Crowding can also elevate the concentrations of conspecific or competitor exudates, metabolites and excretory substances in the water column (Hobaek & Larsson, 1990; Ban & Minoda, 1994), which promotes resting egg production through the suppression of parthenogenetic reproductive output (Zadereev & Lopatina, 2007) or inhibition of feeding (Lürling *et al.*, 2003). Strickler & Twombly (1975) forwarded a different perspective, in which they highlighted the possibility that freshwater cyclopoids enter diapause in response to elevated invertebrate predation. Through field observations, Hairston, Walton & Li (1983) suggested that the freshwater copepod *Onychodiaptomus sanguineus* (syn. *Diaptomus sanguineus*) abandons the pelagial in spring to remain in the sediment as resting eggs to avoid intense summertime sunfish predation. Fish-induced changes of diapause initiation and seasonal descent have been documented both in the freshwater and marine realms (e.g. Hairston & Dillon, 1990; Kaartvedt, 2000). Through experimental evidence, Ślusarczyk (1995) and Pijanowska & Stolpe (1996) concluded that early developmental stages of *Daphnia* that were exposed to predator (fish) exudates had a greater chance of producing resting eggs in their adult stages.

According to Weismann (1876), the transition from parthenogenetic egg production to resting egg production in *Daphnia* spp. is controlled by an 'internal rhythm' rather than external cues. However, the nature of this internal rhythm remains unclear. Based on the observations on *Pseudocalanus* populations in Loch Striven, Corkett & McLaren (1979) hypothesised that individuals with larger lipid stores descend to overwintering depths earlier in the season, while those with

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

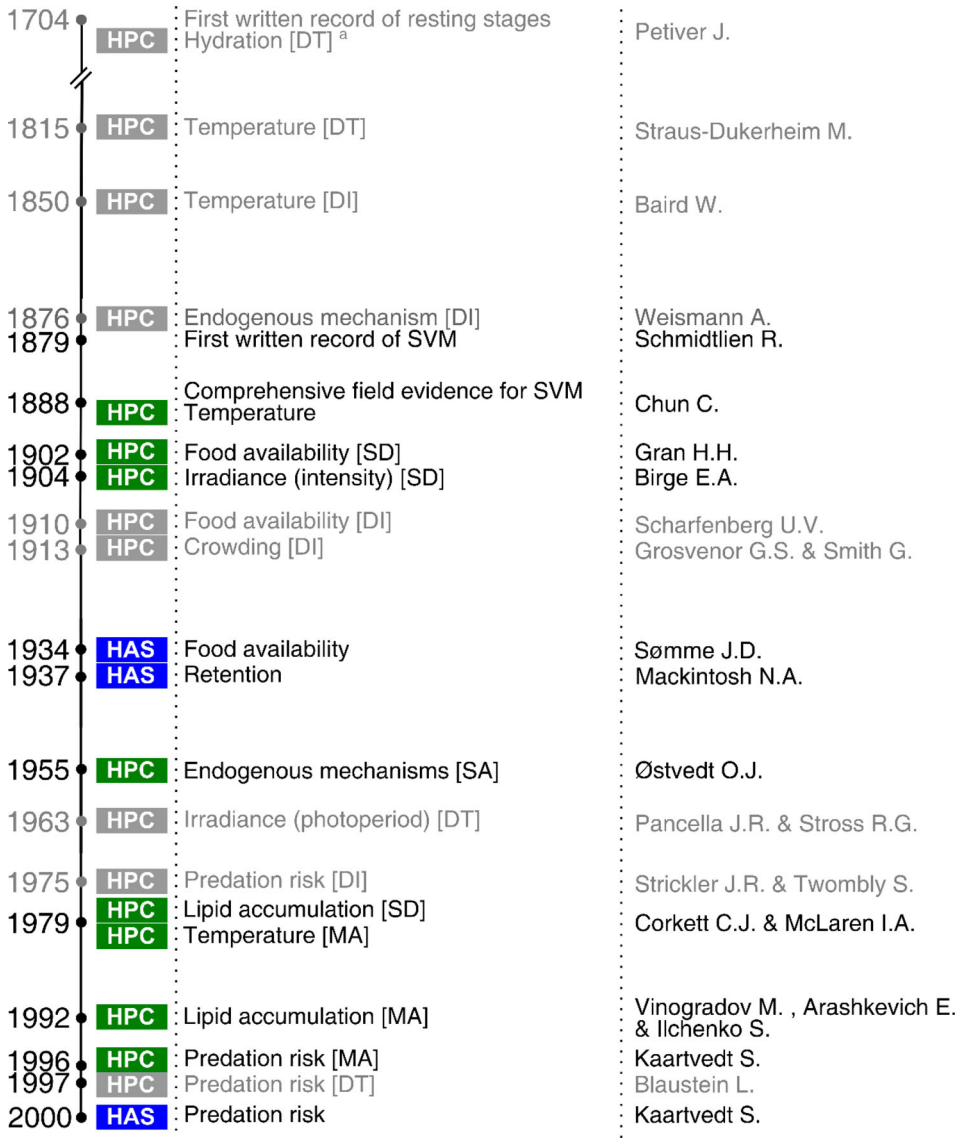

Fig 8. Development of the main hypotheses related to the proximate control (HPC) and adaptive significance (HAS) of seasonal vertical migration (SVM) (indicated in blue and green) and diapause (indicated in grey). DI, diapause induction; DT, diapause termination; MA, migration amplitude; SD, seasonal descent; SA, seasonal ascent. [a]The first written record of hatching of resting eggs, most likely through hydration.

smaller stores continue to develop towards adulthood in an attempt to reproduce within the same calendar year. These arguments were strongly echoed in the later work of Rey-Rassat *et al.* (2002), who hypothesised that high-latitude calanoid copepods perform their seasonal descent after accumulating 'sufficient' energy reserves for overwintering (the lipid accumulation window hypothesis). According to the conceptual model of Irigoien (2004), the sufficient (threshold) lipid level that triggers the seasonal descent may be individual-specific, which is a trait that varies within the population. Irigoien (2004, p. 261) wrote: "*This hypothesis suggests that year after year the depth of the convective mixed layer and the timing of the bloom will be a strong source of natural selection, leaving animals that get their lipid level wrong without offspring*". Although criticised for its over simplicity (see Campbell, 2004; Fiksen, Varpe & Kaartvedt, 2004), recent field evidence indicates that an influence of the size of lipid reserves on the timing of seasonal descent cannot be overlooked (Johnson *et al.*, 2008; Schmid, Maps & Fortier, 2018). Potential lipid thresholds are most easily understood and predicted for income breeders, while lipid levels should be more variable and plastic if the lipid reserves are also intended for reproduction the following spring (Varpe & Ejsmond, 2018*b*).

(ii) Hypotheses about diapause termination and seasonal ascent. In the early 18th century, British entomologist James Petiver noted that he was able to hatch resting eggs

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

of the fairy shrimp *Chirocephalus diaphanus* (syn. *Squilla lacustris minima*, *dorso natante*) (Petiver, 1704). As these eggs are buried in the sediment and withstand prolonged droughts (Bratton & Fryer, 1990), Petiver likely used a rehydration technique (e.g. incubate in water) to hatch them. In fact, short- or long-term hydration is the main cue for diapause termination of zooplankton occupying small ponds that seasonally dry out (e.g. Calman, 1909; Green, 1919; Wood, 1932; Fryer, 1997; Spencer & Blaustein, 2001*b*; Rossi *et al.*, 2012). In perennial freshwater systems, such as large ponds and lakes, the termination of diapause and the seasonal ascent of resting stages appears to be triggered by seasonal variations of temperature (e.g. Cooley, 1971; Marcus, 1980; Uye, 1980; Schwartz & Hebert, 1987; Maier, 1990). Laboratory experiments in this regard date back to the early 19th century. For example, according to Straus-Dukerheim (1815), the hatching success of *Daphnia* resting eggs increases when incubated at typical summertime temperatures. Similarly, Pancella & Stross (1963) observed a substantial improvement in the hatching success of *D. pulex* resting eggs when incubated at room temperature. While the spring–summer increase in photoperiod is a likely cue for hatching of resting eggs of many freshwater zooplankton (e.g. Shan, 1970; George, 1973; Gyllström, 2004), the springtime increase in irradiance intensity has been suggested as a proximate cue for the seasonal ascent of high-latitude calanoid copepods in relatively deep marine environments (e.g. Bigelow, 1926; Sømme, 1934; Ussing, 1938; Grigg & Bardwell, 1982).

In a study of deep seasonal migrations of *Calanus* spp. in the Norwegian Sea, Østvedt (1955, p. 45) doubted that irradiance or temperature could act as proximate cues for their seasonal ascent. He wrote: "*But whether variations of temperature affect the sign of geotropic reactions or not, this cannot be the explanation of the spring ascent of copepods at station-M, as in the 1000 m level the temperature was almost constant during the whole year [……] phototactic responses cannot occur at depths where the illumination is so diffuse that its direction is no longer perceptible to the copepod*". Instead, Østvedt (1955) suggested the gradual development of overwintering stages and approach towards sexual maturity as the likely trigger for the spring ascent and called it a 'spawning migration'. However, Østvedt's observations were mainly for the copepod *C. finmarchicus*, which mostly overwinters at a near-adult copepodite stage (CV; reviewed in Falk-Petersen *et al.*, 2009). Spawning migration thus does not explain the seasonal ascents of early copepodite stages (CIII, CIV) and adult females of other high-latitude *Calanus* congeners, such as *C. glacialis* and *C. hyperboreus* (Dawson, 1978; Hirche *et al.*, 1994; Kosobokova, 1999).

The focus on the role of endogenous mechanisms in diapause termination and seasonal ascent considerably expanded in the 20th century, underpinning two general observations: first, the prevalence of diapause termination and seasonal ascent in the absence of obvious environmental cues (Smyly, 1961, 1962; Conover, 1965) and second, the pronounced variability in the timing of diapause termination within many freshwater and marine zooplankton populations (Miller *et al.*, 1991; Rossi *et al.*, 2012). Carlisle & Pitman (1961) studied neurosecretions of the high-latitude copepods *Calanus helgolandicus* and *C. finmarchicus* and invoked the role of endocrinal regulation of diapause termination. Subsequent studies highlighted the significance of endogenous circannual timers (annual biological clocks) in diapause termination and seasonal ascent of several zooplankton taxa (e.g. Elgmork, 1967; Uye, 1980; Miller *et al.*, 1991; Williams-Howze & Coull, 1992; Campbell, Boutillier & Dower, 2004). Although the molecular basis of an endogenous circannual timer remains uncertain, recent studies point to differential gene expression patterns between diapausing and non-diapausing populations of calanoid copepods. For example, while genes related to lipid synthesis and metabolism, moulting, digestive enzyme activity and photoreception appear to be down-regulated (suppressed) among copepods in diapause, those related to stress regulation and moulting prevention (e.g. the ecdysteroid receptor, *EcR*) are highly up-regulated (expressed) in non-diapausing individuals (Tarrant *et al.*, 2008; Seear *et al.*, 2009; Aruda *et al.*, 2011; Häfker *et al.*, 2018; Skottene *et al.*, 2019). Although endogenous mechanisms are still not widely studied, they appear to prevent unnecessary prolongation of diapause in habitats deprived of environmental cues (Harris, 1963; Dahms, 1995).

The ability of predators to terminate diapause and drive diapausing populations away from the deeper pelagic and benthic habitats is not well studied. However, predator presence can override the influence of other exogenous and endogenous cues. For example, Blaustein (1997) noted a significant hatching delay in the resting eggs of the copepod *Arctodiaptomus similis* and the cladoceran *Ceriodaphnia quadrangular* when near-eastern fire salamander larvae (*Salamandra infraimmaculata*) were present in the environment. Since the experimental results did not change when salamander larvae were caged in a meshed enclosure, it is possible that exudates from the predator provided chemical signals to the resting eggs that led to prolonged diapause. Predator-induced hatching delays of resting eggs were also observed among clam shrimps (Spencer & Blaustein, 2001*a*) and fairy shrimps (De Roeck, Artois & Brendonck, 2005). In two recent wintertime studies conducted in the high-Arctic, Daase, Varpe & Falk-Petersen (2013*b*) and Błachowiak-Samołyk *et al.* (2015) observed large numbers of calanoid copepods in the upper pelagial. Although the authors invoked the possibility of pelagic invertebrate predators (e.g. chaetognaths) driving the overwintering copepods towards the upper pelagial, it was not extensively tested.

Bioturbation, the turbulent mixing of sediments *via* biological processes (Meysman, Middelburg & Heip, 2006) can either promote or demote diapause termination by exposing or masking the benthic resting stages from environmental cues (Brendonck & De Meester, 2003; Gyllström & Hansson, 2004). In an experimental study, Marcus & Schmidt-Gengenbach (1986) observed contrasting roles played by different benthic polychaetes in the hatching success of resting eggs of the marine copepod *Labidocera aestiva*. Bioturbation caused by polychaetes tended to bury the

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

resting eggs several centimetres down in the sediment, where they were not able to hatch. Conversely, eggs translocated toward the sediment–water interface through accidental ingestion and defecation by polychaetes had a greater chance of hatching, since they remained viable after predator gut passage and were exposed to environmental cues (e.g. irradiance and temperature) upon settling on the sediment–water interface.

(iii) Hypotheses about migration amplitude (vertical habitat selection). The SVM amplitude of resting stages that sink passively to the bottom is solely constrained by the water depth. A fraction of these resting stages can settle on macrophytes and may not reach the sediment (Caceres & Hairston, 1998). Resting stages that actively swim to the sediment can burrow several centimetres into it, causing their seasonal migration to transit across both pelagic and benthic habitats. For example, Elgmork *et al.* (1990) studied the SVM patterns of the planktonic cyclopoids *Cyclops scutifer* and *Mesocyclops leuckarti* and found that they burrow into anaerobic sediments prior to the initiation of diapause. Occupying anaerobic habitats during the several-months-long diapause can significantly increase the chances of survival, since many predators tend to avoid oxygen-deficient habitats (Gyllström & Hansson, 2004). Most zooplankton that overwinter in the deep pelagial can tolerate lower oxygen concentrations through elevated production of the oxygen-transport metalloprotein haemoglobin (Weider & Lampert, 1985; Sell, 1998). They can also withstand higher concentrations of toxic sulfidic compounds that are common in deeper waters (Borcherding *et al.*, 2017). Therefore, zooplankton are generally capable of venturing into deeper waters than their predators (Voss & Mumm, 1999; Larsson & Lampert, 2011). Although overwintering migrations of some high-latitude fjord zooplankton populations are seen as predator-avoiding strategies (Kaartvedt, 1996; Dale *et al.*, 1999), whether selection of deep overwintering habitats is driven by low ambient oxygen concentrations is not yet fully known. It is more likely that deep pelagial overwintering is a light-mediated predator-avoidance behaviour, since darker deep waters can hamper the detection efficiency of visually orientating planktivores (e.g. Gislason & Astthorsson, 2002; Gislason, 2003; Sentyabov & Prokopchuk, 2006).

Temperature plays a key role in the vertical habitat selection of overwintering zooplankton. According to Corkett & McLaren (1979), the preference for colder water masses by the high-latitude *Pseudocalanus* spp. during overwintering is a strategy that reduces their metabolic rate and conserves energy reserves. Hirche (1991) described the contrasting vertical distributions of *Calanus* spp. in the eastern and western boundaries of the Fram strait in relation to temperature. On the eastern side, copepods of genus *Calanus* avoided the upper pelagial dominated by warmer Atlantic water masses and overwintered between 500 and 1500 m in the colder waters off the western Spitsbergen shelf. However, the vertical distribution of *Calanus* spp. was shallower (<500 m) in the western side of the Fram strait, where colder polar waters dominated the upper pelagial. As observed in numerous subsequent studies, the tendency of North Atlantic and Arctic *Calanus* spp. to occupy colder water masses during overwintering likely reflects the need for these ectotherms to conserve their energy reserves at a reduced metabolic cost (Heath & Jónasdóttir, 1999; Astthorsson & Gislason, 2003; Halvorsen *et al.*, 2003; Heath *et al.*, 2004). Occupation of colder waters during typically 4–6 months of overwintering is an essential survival strategy for predominantly herbivorous zooplankton, since their lipid reserve is probably the sole wintertime energetic input (Ingvarsdóttir *et al.*, 1999; Grosbois *et al.*, 2017; Schneider *et al.*, 2017).

According to Vinogradov, Arashkevich & Ilchenko (1992), the overwintering habitat selection of seasonally migrating high-latitude copepods is influenced by water density, where they settle at a depth that provides neutral buoyancy. Vinogradov *et al.* (1992, p. 457) wrote: "*the thin layer (or two layers) with the maximal* Calanus *concentration often appears to be timed perfectly to the same 'niches', which gives them an opportunity to reduce mobility to a minimum and with it use of energy, enabling them to survive the winter diapause more efficiently*". This idea was further developed by Visser & Jónasdóttir (1999) who suggested a buoyancy-driven overwintering habitat selection mechanism for high-latitude calanoid copepods. Accordingly, lipid-rich copepods (typically CIV or CV stages) swim down against positive buoyancy to a depth where neutral buoyancy is attained, which becomes their overwintering habitat. The maintenance of neutral buoyancy at greater depths may be attained *via* two mechanisms. First, unsaturated wax esters, a crucial component of the lipid store of many high-latitude zooplankton (Lee, Hagen & Kattner, 2006), undergo a liquid-to-solid phase transition typically at depths below 500 m (Pond & Tarling, 2011). This allows some zooplankton (e.g. the copepods *Calanus finmarchicus* and *Calanoides acutus*) to compensate positive buoyancy forces, since solidified unsaturated wax esters are denser compared to their liquid phase (Clark, Brierley & Pond, 2012; Pond *et al.*, 2012). Second, copepods likely compensate negative buoyancy forces by replacing ions with heavier molecular mass (e.g. Na^+, Mg^{2+}) with those of lighter molecular mass (e.g. NH_4^+) in their haemolymph (Sartoris *et al.*, 2010). Negative buoyancy forces may also be countered *via* selective catabolisation of unsaturated wax esters during overwintering (Clark *et al.*, 2012). However, the roles of ionic exchange and phase transition of wax esters in overwintering habitat selection of high-latitude copepods are still not widely agreed (see Pond & Tarling, 2013; Wilson, Speirs & Heath, 2013) and further studies are required to test the generality of these hypotheses.

(*b*) Hypotheses about the adaptive significance of SVM

In ephemeral freshwater habitats that annually dry out, diapause may ensure the long-term survival of the pelagic inhabitants. In perennial lakes and marine environments, SVM and diapause are essential for surviving predictable annual degradation of habitat quality, especially the termination of primary production (Sømme, 1934; Mariash, Cusson & Rautio, 2017) and increased predation risk (Strickler &

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Twombly, 1975; Hairston *et al.*, 1983; Kaartvedt, 2000; Varpe & Fiksen, 2010).

When the habitat quality varies dramatically within and between years, the production of resting stages becomes a conservative bet-hedging strategy (Cohen, 1966; Hairston & Fox, 2009). While some of these resting eggs may hatch within a shorter timespan (e.g. the following year) others may remain dormant for many years, thus adding to an egg bank (Brendonck & De Meester, 2003). Egg banks are useful for population persistence during prolonged periods of environmental extremes, such as droughts and pollution events (Carlisle, 1968; Belk, 1970; Novikova *et al.*, 2011). For example, the native pelagic community (phytoplankton, zooplankton and fish) of an Italian lake (Lake Orta) were decimated due to unprecedented industrial discharge of copper and ammonium sulphate during the late 1920s (Bonacina & Pasteris, 2001; Calderoni & Tartari, 2001). However, core samples taken from the deep parts of the lake (*ca.* 150 m) showed an abundance of zooplankton resting eggs (Piscia *et al.*, 2016). Owing to conservation efforts, the lake ecosystem was restored during the late 1980s, and several years later, the zooplankton community reappeared in the pelagial. Despite the loss of habitat quality of the pelagial, the zooplankton community of lake Orta survived due to the persistent egg bank and recolonised the pelagial upon environmental restoration (Piscia *et al.*, 2016; Zweerus *et al.*, 2017).

SVM also can promote zooplankton dispersal. Benthic resting stages of zooplankton inhabiting lakes and ponds that seasonally dry out are dispersed by the wind and likely colonise adjacent aquatic habitats (Brendonck & Riddoch, 1999; Vanschoenwinkel *et al.*, 2008). Resting stages can also be transported across different habitats by aquatic insects (e.g. Lansbury, 1955; Van de Meutter, Stoks & De Meester, 2008), fish (e.g. Antsulevich & Välipakka, 2000; Jarnagin, Swan & Kerfoot, 2000; Hansson, Fagerberg & Gorokhova, 2004), birds (e.g. Malone, 1965; Proctor, Malone & DeVlaming, 1967; Frisch, Green & Figuerola, 2007), amphibians (e.g. Brown, 1933; Mellors, 1975) and mammals (e.g. Allen, 2007) either through gut passage or attachment mechanisms. Conversely, the SVM of overwintering zooplankton in deeper waters is sometimes regarded as a mechanism of geographic redistribution. For example, Mackintosh (1937) studied SVM patterns of many zooplankton species in relation to the horizontal movement of water masses in the Southern Ocean and suggested that the summertime inhabitants of northward-moving Antarctic surface waters are returned as they descend to overwinter in southward-moving Antarctic deeper water. Mackintosh (1937, p. 380) wrote: "*We have evidence then of a general circulation on a very large scale, the majority of organisms drifting northwards in the surface layers in summer and returning southwards in the warm deep water in winter*". SVM-driven retention or dispersal mechanisms have been suggested for ice-associated amphipods in the central Arctic ocean (Berge *et al.*, 2012), copepods occupying higher latitudes (Irigoien, 2004) and coastal upwelling zones (Peterson *et al.*, 1979; Verheye *et al.*, 1991). The production of resting eggs may also aid retention in upwelling environments. For example, Marcus (1995) observed large aggregates of benthic resting eggs of the marine calanoid copepod *Acartia clausi* in the Northern California Current upwelling system and suggested that it may be a strategy to remain in these seasonally productive waters.

(4) Plasticity of SVM

The periodicity and amplitude of SVM often vary between geographic locations, time, habitats, species and individuals. This variability is partly driven by the seasonal dynamics of physical environmental variables, such as temperature (e.g. Hirche, 1991; Astthorsson & Gislason, 2003; Halvorsen *et al.*, 2003; Bernot *et al.*, 2006), food availability (Herman, 1983; Head & Harris, 1985; Hansen & Hairston, 1998; Hind *et al.*, 2000), predation risk (e.g. Hairston & Walton, 1986; Kaartvedt, 1996; Fernö *et al.*, 1998), water clarity, bottom depth and topography (e.g. Bagøien *et al.*, 2001; de Senerpont Domis *et al.*, 2007; Slagstad & Tande, 2007; Dupont & Aksnes, 2011). For example, when environmental conditions become potentially harmful (e.g. due to pollution and predation), diapause termination and seasonal ascent of resting stages may be delayed for several years or decades (Madhupratap *et al.*, 1996). On the other hand, in environments with brief and highly unpredictable food supply, a single individual may perform several annual vertical excursions before reaching sexual maturity (Dawson, 1978; Hirche *et al.*, 1994). The interspecific variability in the timing and amplitude of SVM largely underpins differential body sizes (and size-specific predation risk), foraging tactics and reproductive strategies (Hairston, Olds & Munns, 1985; Norrbin, 1996; Madsen, Nielsen & Hansen, 2001; Darnis & Fortier, 2014; Bandara *et al.*, 2016). For example, in some fjord communities of North Atlantic and Arctic *Calanus* spp., the timing of the seasonal ascent occurs earliest in *C. hyperboreus*, whose egg production does not rely on food availability (Plourde *et al.*, 2003; Henriksen *et al.*, 2012) – a reproductive strategy termed capital breeding (Varpe *et al.*, 2009). Using stored energy reserves, *C. hyperboreus* produce eggs at overwintering depths prior to the commencement of pelagic algal bloom, which gradually ascend to the surface due to positive buoyancy (Hirche & Niehoff, 1996). By contrast, *C. finmarchicus* ascends from overwintering depths relatively later in the season since it has to feed on pelagic algae to fuel its spawning (Marshall & Orr, 1972; Hirche, 1996*b*), termed income breeding (Varpe *et al.*, 2009). The seasonal ascent of *C. glacialis* may occur in between the two other congeners (e.g. Madsen *et al.*, 2001; Arnkværn, Daase & Eiane, 2005) since it follows an intermediate breeding strategy, where the egg production is fuelled partly by energy reserves and partly by feeding on ice-associated and pelagic algae (Søreide *et al.*, 2008; Daase *et al.*, 2013*a*). These are mixed breeders in terms of capital and income (*cf.* Varpe & Ejsmond, 2018*b*). The variability of timing and amplitude of SVM observed between individuals of the same species is largely dependent on their

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

nutritional state and the size of the lipid reserve (Pedersen, Tande & Ottesen, 1995; Johnson *et al.*, 2008; Schmid *et al.*, 2018) – a finding also predicted by several models (e.g. Varpe *et al.*, 2009).

(5) Community and ecosystem consequences of SVM

SVM patterns of the herbivore zooplankton community are often followed by pelagic predators of both invertebrate (e.g. Sullivan, 1980; Terazaki & Miller, 1986; Samemoto, 1987; Larson & Harbison, 1989; Siferd & Conover, 1992; Torres *et al.*, 1994*b*; Lundberg *et al.*, 2006; Purcell *et al.*, 2010; Grigor, Søreide & Varpe, 2014) and vertebrate origin (e.g. Bagøien *et al.*, 2001; Sims *et al.*, 2003; Shepard *et al.*, 2006; Geoffroy *et al.*, 2011). Lipids accumulated in the upper pelagial during the productive season are brought to depths by overwintering individuals (e.g. high-latitude *Calanus* spp.) and provide an important source of energy for an array of carnivores, such as mesopelagic fishes. Energy sourced from these lipids flows along trophic chains and may be consumed by apex predators, such as marine mammals, seabirds, polar bears and humans (Falk-Petersen *et al.*, 2007; Wirta *et al.*, 2015; Eysteinsson *et al.*, 2018). The earliest comprehensive record of the trophic-wide implications of zooplankton SVM was probably documented by Macdonald (1927). He collected vertical net hauls in the Firth of Clyde and found large numbers of younger developmental stages of the euphausiid *Meganyctiphanes norvegica* (northern krill) in shallow waters in spring and summer. In the late winter, most of the *M. norvegica* population had descended below 100 m, and their gut contents largely comprised remnants of the copepod *Calanus finmarchicus* and detritus. Since *M. norvegica* is an omnivore that switches between a phytoplankton and zooplankton diet (Schmidt, 2010), Macdonald suggested that the euphausiid followed the overwintering migration of *C. finmarchicus* to greater depths. Macdonald (1927) further cited the contemporary observations made in Norwegian Fjords and Gulf of Maine about sudden wintertime surfacing of *M. norvegica*, possibly driven upwards from their deep wintertime feeding habitats by Atlantic pollock (*Pollachius virens*). Such studies are rare because most high-latitude field investigations seldom focus beyond one or two trophic levels. For example, David (1956) noted that the seasonal changes of the vertical distribution of the chaetognath *Pseudosagitta gazellae* was due to seasonally following their copepod prey. However, he did not study how this vertical behaviour could influence their predators (e.g. planktivorous fish). Similarly, in a recent year-round study, Bandara *et al.* (2016) derived statistically significant associations among seasonal vertical distributions of prey and predator zooplankton taxa across three adjacent trophic levels. Nonetheless, their investigation did not sample the pelagic fish community, and thus overlooked the seasonal vertical dynamics at higher ends of the food chain.

Seasonally migrating zooplankton play a prominent role in the deep-ocean carbon sequestration process. The lipid reserves accumulated by herbivore zooplankton in spring and summer are carried down into the deep ocean during their autumn–winter descent. At these depths, stored lipids are metabolised typically at a rate accounting for *ca.* 25% of the basal metabolic rate (Maps *et al.*, 2013). Despite the reduced metabolism, a 6–8 month-long overwintering period can exhaust a substantial fraction (44–93%) of the stored lipids (Jónasdóttir *et al.*, 2015). Further, only a part of the overwintering population ascends to the near-surface waters in the following spring, while the rest are either consumed by deep-dwelling predators or die due to starvation, disease and other sources of mortality (Bagøien *et al.*, 2000; Arnkværn *et al.*, 2005; Gislason, Eiane & Reynisson, 2007; Daase *et al.*, 2013*b*). The lipid-based carbon flux driven by the zooplankton SVM (the 'lipid pump') is thus a largely unidirectional process that transports carbon directly to the deep ocean with little losses on the way (Jónasdóttir *et al.*, 2015; Visser, Grønning & Jónasdóttir, 2017). Longhurst and Williams (1992) made the first attempt to quantify the lipid pump in the North Atlantic and suggested that its contribution to the total particulate organic carbon flux is insignificant (estimated at 0.275 g C m^{-2} $year^{-1}$ by *Calanus* spp.). However, recent estimates of <11.5 g C m^{-2} $year^{-1}$ by Jónasdóttir *et al.* (2015) and 2.0–6.0 g C m^{-2} $year^{-1}$ by Jónasdóttir *et al.* (2019) for the North Atlantic *C. finmarchicus* and 3.5–6.0 g C m^{-2} $year^{-1}$ by Visser *et al.* (2017) for *C. hyperboreus* suggest that the initial figures are likely significant underestimates. These updated North Atlantic SVM-driven carbon flux estimates are in line with those made elsewhere, such as the estimated 3.1 g C m^{-2} $year^{-1}$ in the Amundsen Gulf for *Calanus* spp., 1.965–4.3 g C m^{-2} $year^{-1}$ in the Western subarctic Pacific for *Neocalanus* spp. (Kobari, Shinada & Tsuda, 2003; Kobari *et al.*, 2008) and 1.7–9.3 g C m^{-2} $year^{-1}$ in the Southern Ocean for *N. tonsus* (Bradford-Grieve *et al.*, 2001).

IV. METHODS OF STUDYING ZOOPLANKTON VERTICAL MIGRATIONS

Methods of studying zooplankton vertical migrations have developed significantly over the past two centuries and can be classified into three broad categories: (*i*) sampling or collection methods, (*ii*) *in-situ* observation methods, and (*iii*) tracking and simulation methods.

(1) Sampling methods

The classic method for studying vertical migrations involves sampling zooplankton populations from different depths and interpreting changes in their vertical distributions as migratory patterns (Pearre, 1979). Some of the commonly used sampling devices include towed nets, traps and pump systems. The preferred device may differ notably between marine and freshwater realms, primarily due to differences

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

in turbidity, flow regimes, bottom topography and depth dynamics.

(*a*) Sampling in marine systems

The earliest evidence of zooplankton vertical migration originated from samples collected from the upper pelagial using simple plankton nets. For example, Charles Darwin's hypothesis that pelagic animals retreat from the upper pelagial due to wave action was based on samples collected using a simple plankton net during the *Beagle* survey voyage (Darwin, 1833). Since these early net designs lacked a closing mechanism, they did not uncover the vertical dimensionality of the migration and the descriptions were solely based on the periodic appearance and disappearance of zooplankton from the upper pelagial. Fuchs (1882) and Chun (1888) used primitive opening/closing nets to obtain depth-stratified samples and provided initial insights about the amplitude of diel and seasonal vertical migrations. Due to the cumbersome nature of sampling several depth layers with a single net, the use of dual net systems became popular during the first half of the 20th century. Hoyle (1889) used probably the first dual opening/closing net system, in which each net could be closed independently using two separate weighted messenger and cable systems. The first vertically towed multiple net system, termed the Multiple Plankton Sampler (MPS) with four sequentially opening/closing nets was developed by Bé, Ewing & Linton (1959). The weighted messenger and cable system of the MPS was later refitted with a pressure-actuated closing mechanism by Bé (1962). MPS was further improved by Weikert & John (1981) to carry five vertically towed nets and equipped with a programmable electronic release mechanism. This device, commercially known as the MultiNet (Hydro-Bios, Kiel), is widely used today to take depth-stratified zooplankton samples both in shallow coastal water bodies, such as estuaries and fjords (e.g. Criales-Hernández *et al.*, 2008; Daase, Hop & Falk-Petersen 2016) and deeper ocean basins (e.g. Auel *et al.*, 2003; Gaardsted, Tande & Basedow, 2010). Apart from vertically towed nets, obliquely towed multiple net systems are also commonly used to study zooplankton vertical migrations. One of the pioneering designs is the Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe *et al.*, 1976). The MOCNESS includes up to 10 electronically operated nets and carries an array of sensors for environmental monitoring (e.g. temperature, fluorescence, dissolved oxygen and irradiance sensors). The initial MOCNESS design was improved and upscaled in a number of recent developments, such as the Bedford Institute of Oceanography Net and Environmental Sensing System (BIONESS; Sameoto, Jaroszynski & Fraser, 1980) and the Large Opening/Closing High-Speed Net and Environmental Sampling System (LOCHNESS; Dunn *et al.*, 1993*b*).

Early efforts to minimise the avoidance of towed nets by larger zooplankton included the design of downward-falling nets (e.g. Buchanan-Wollaston, 1911; Heron, 1982). However, these free-falling nets are not widely used today, and instead, net avoidance is typically reduced by increasing the towing speed (Skjoldal *et al.*, 2013) or mounting powerful strobe lights at the front of the net (Wiebe *et al.*, 2004). Due to the availability of a diversity of plankton nets with varying dimensions and mesh sizes, some form of standardisation was required to reduce variability of zooplankton sampling among scientific investigations (Motoda, Anraku & Minoda, 1957). In 1968, the International Council for the Exploration of the Seas (ICES), Scientific Committee on Oceanic Research (SCOR) and United Nations Educational, Scientific and Cultural Organization (UNESCO) jointly published standards for zooplankton sampling in the marine realm, most of which are currently in use (Fraser, 1968). Accordingly, a net with a smaller opening (0.25 m^2) and a mesh width of 200 μm vertically towed at moderate speeds (ca. 0.5 ms^{-1}) was adopted to capture smaller mesozooplankton (WP-2 net). For capturing larger mesozooplankton and macrozooplankton, a fast-towed net (*ca.* 1 ms^{-1}), with a larger mouth opening (1 m^2) and larger mesh width (1000 μm) was adopted (WP-3 net). For capturing smaller zooplankton (e.g. microzooplankton), water bottle samplers, pump systems and nets with smaller mesh widths (50–70 μm) were suggested.

A different class of plankton-collecting devices called 'high-speed plankton samplers' emerged in the late 19th century. High-speed plankton samplers are towed in the upper pelagial typically at speeds of 1–12 ms^{-1} over long distances, during which zooplankton are strained using nets and preserved within the sampler itself (Wiebe, Bucklin & Benfield, 2017). Most high-speed samplers, such as the Continuous Plankton Recorder (CPR; Hardy, 1935), Longhurst-Hardy Plankton Recorder (LHPR; Longhurst *et al.*, 1966) and Autosampling and Recording Instrumented Environmental Sampling System (ARIES; Dunn *et al.*, 1993*a*) operate at prescribed depths in the upper pelagial and thus do not produce data with vertical resolution. Consequently, descriptions of zooplankton vertical migrations from high-speed samplers are based on the periodic appearance and disappearance of zooplankton in the upper pelagial. Such data are nonetheless useful, as in a recent study, Strand *et al.* (2020) used 8 years of CPR data collected in Nordic Seas and described a previously undocumented fraction of the *Calanus finmarchicus* population that occupy warmer Atlantic water masses of the Norwegian and Icelandic Seas until autumn and descend relatively late for overwintering. At the time of writing, CPR has been towed for nearly 16 million kilometres (https://www.cprsurvey.org/) and contributed significantly to the development of the zooplankton vertical migration knowledgebase.

(*b*) Sampling in freshwater systems

Although Cuvier (1817) was the first to document the DVM of *Daphnia*, the method that he used to observe it remains unclear. The use of nets to collect freshwater zooplankton appears in the literature in the late 19th century (Birge, 1882; Forbes, 1882). To minimise the loss of

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

zooplankton through the net's mesh and to account for the inability to capture zooplankton in a preferred depth stratum, Juday (1916) developed a pelagic zooplankton sampler termed the Juday plankton trap. The trap is lowered into the water column with its top and bottom doors open, and when the desired depth is reached, a messenger is released along a cable to close the doors. The trap is then hauled to the surface and the sample (*ca.* 5 l) is drained and filtered. Juday's initial design received several iterative upgrades (e.g. Juday, 1926) and was significantly modified by Clarke (1942). This design has ultimately evolved into an array of pelagic plankton traps, such as the Rüttner sampler (Ruttner, 1953), Schindler–Patalas trap (Patalas, 1954; Schindler, 1969) and its subsequent modifications. High-speed samplers were introduced to freshwater systems in the late 1960s. For example, Swain (1970) used a Continuous Plankton Recorder and a Multi-depth Plankton Indicator to obtain depth-stratified zooplankton samples in lakes Superior, Michigan and Huron, and described vertical migration patterns of numerous zooplankton taxa. Later, Swain & Roijackers (1985) developed a downscaled version of the Multi-depth Plankton Indicator to investigate vertical migration of crustacean zooplankton in smaller lakes.

High-speed samplers are not necessary in lotic (moving water) systems, as zooplankton can be collected easily in the downstream flow using mounted plankton nets ['drift samplers' (Cushing, 1964; Field-dodgson, 1985)]. However, plankton nets and traps deployed in lotic systems, especially under high-turbidity, fast-flowing conditions often encounter operational difficulties, such as clogging and towing inconsistencies (McQueen & Yan, 1993; Mack *et al.*, 2012). Therefore, pump systems are generally better suited for sampling in lotic waters. For example, in a recent study conducted in the Upper Mississippi River, Appel *et al.* (2020) compared the sampling efficiency and operational practicability of a Schindler–Patalas trap (volume = 30 l), an integrated tube sampler (diameter = 50 mm, length = 50 cm), diaphragm pump (diameter = 13 mm, length = 2 m) and a tow net (opening ≈ 0.20 m^2, mesh width = 504 μm). Collections using the pump system yielded the highest numerical abundance. Although the Schindler–Patalas trap produced somewhat comparable abundance estimates to the pump system, its operation in fast-flowing sections of the river was compromised by water currents. The plankton net produced a lower estimate of zooplankton abundance but captured a broad spectrum of lifeforms. Despite being operationally convenient, the tube sampler significantly underestimated the abundance and species richness of the investigated riverine zooplankton community.

(2) *In-situ* observation methods

The sampling of zooplankton is a destructive method and requires labour-intensive enumeration and identification steps to be completed before quantitative estimates of vertical migration can be produced. An alternative is to observe zooplankton in their natural habitats, typically using acoustic and optical techniques.

(*a*) Acoustic observations

(i) Acoustic observations in marine systems. The earliest acoustic device for depth detection was invented by the Norwegian Hans Sundt Berggraf, who published in the *Teknisk Ukeblad* (Technical Weekly) in 1904 under the translated title *An apparatus by which the depth of the sea can be measured, without the apparatus being connected to the seabed* (Berggraf, 1904). However, it was the German physicist Alexander Bhem who patented this device almost a decade later in 1912 (Behm, 1921). These early echosounders were primarily used for navigational purposes. The use of acoustic devices to detect zooplankton vertical migrations dates to the World War II era, where sonars affixed to German U-boats operating in the Atlantic detected a 'dynamic false bottom' that remained deeper during the daytime and ascended gradually at dusk. Scientific research on this phenomenon was conducted in the early 1940s, and this dynamic false bottom was named the ECR layer, in honour of Carl F. Eyring, Ralph J. Christensen and Russell W. Raitt who provided its first detailed acoustic characterisation (Eyring, Christensen & Raitt, 1948). The ECR layer was later referred to as the Deep Scattering Layer (DSL) and its biological origin was first described by the American oceanographer Martin W. Johnson (Johnson, 1948). He collected depth-stratified net hauls and found large concentrations of zooplankton (e.g. copepods and euphausiids) at depths corresponding to the DSL. Johnson (1948, p. 457) wrote: "*The deep scattering layer has been shown by its diurnal vertical migrations to be biological in nature. The partial reflection of fathometer signals in this layer promises to be a useful ecological tool in studying the organisms involved*".

The technology used for acoustic characterisation of zooplankton and detection of their vertical migrations has advanced rapidly in recent decades (Stanton, 2012). For example, the early single-beam echo sounders could only estimate the integrated energy returning from all sound scatterers in a given ensonified volume (i.e. the volume backscattering intensity). In addition, multi-beam systems can detect the backscattering strength of individual sources in the ensonified volume (i.e. the target strength) and thus allow tracking of individuals across space and time (Ehrenberg, 1974; Greene, Wiebe & Burczynski, 1989; Wiebe & Benfield, 2003). Further, the development of modelling techniques to interpret backscattering signals (e.g. frequency-dependent characterisation of lifeforms) has advanced significantly in recent times (reviewed in Lavery *et al.*, 2007). Recent developments in high-resolution broadband acoustics have enabled the seamless use of a wide range of sound frequencies (e.g. 1–1000 kHz) for the detection, monitoring and tracking of zooplankton and fish using a single echosounder (Lavery & Stanton, 2016; Lee, Chu & Dosso, 2019). For example, in a recent study, Skaret *et al.* (2020) used a broadband echosounder to monitor diel vertical behaviour across multiple trophic levels, including krill (*Thysanoessa* spp.),

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

capelin (*Mallotus villosus*), polar cod (*Boreogadus saida*) and adult Atlantic cod (*Gadus morhua*) in the northern Barents Sea (a relatively shallow shelf sea). Their acoustic data showed that the krill performed classic DVM and were followed to deeper waters (*ca.* 150 m) by planktivorous capelin and polar cod at dusk. Predatory Atlantic cod remained in deeper waters and fed on the descending planktivores, thus providing a daytime refuge for the vertically migrating krill.

(ii) Acoustic observations in freshwater systems. The use of acoustic devices to observe freshwater zooplankton dates to the late 1960s, when McNaught (1969) used a side-scanning echosounder system to characterise the cladoceran populations inhabiting the North American Great Lakes. The effectiveness of acoustic devices in estimating the abundance and vertical distribution of freshwater zooplankton was tested rigorously during the 1980s and 1990s (e.g. Morton & MacLellan, 1992; Smith *et al.*, 1992; Greenlaw, Player & Samilo, 1994). Although not as widespread as in the marine realm, acoustic techniques to observe lacustrine populations of zooplankton and fish have gained popularity over the past two decades. For example, Hembre & Megard (2003) used a 192-kHz side-beam sonar device to study the spatio-temporal habitat selection strategies of the cladoceran *Daphnia pulicaria* and the planktivore rainbow trout (*Oncorhynchus mykiss*) in Long Lake, Minnesota. During daytime, *D. pulicaria* aggregated in dense patches in a deep-water 'refuge zone' where oxygen concentrations were low (3–5 mg l^{-1}), which was below the typical tolerable range of the planktivore. Similarly, Warren, Leach & Williamson (2016) observed likely predator-driven dense patches of cladocerans and copepods across four lakes in Sierra Nevada, California using two simultaneously deployed single-frequency echosounders operating at 120 kHz and 710 kHz frequencies.

(*b*) Optical techniques

In the early 1950s, a group of Japanese scientists used a device called the 'Kuroshio undersea observation chamber' to obtain *in-situ* photographs of zooplankton in the Sea of Japan (Inoue, Saskai & Oaki, 1953). Nishizawa, Fukuda & Inoue (1954) used these photographs to analyse the swimming patterns and speeds of zooplankton. The use of imaging techniques to observe the inhabitants of DSLs became widespread from the mid-1950s onwards (e.g. Edgerton & Hoadley, 1955; Backus & Barnes, 1957; Myrberg & Arthur, 1973). While these early imaging instruments predominantly facilitated qualitative work, the development of the Video Plankton Recorder (VPR) allowed the observation of zooplankton in a defined volume of water and thus produced quantitative estimates of zooplankton abundance and vertical distribution (Davis, Gallager & Solow, 1992). For example, Sainmont *et al.* (2014) used a VPR alongside a CTD (Conductivity, Temperature and Depth device) and an irradiance sensor to profile the water column of Disco Bay, Greenland covering an entire diel cycle. They observed a classic DVM pattern among copepods (*Calanus* spp.) that followed a preferred light intensity of *ca.* 10^{-9} μmol photons m^{-2} s^{-1} throughout the diel cycle, likely to minimise visual predator encounters. The VPR was subsequently upgraded with digital colour video recording, on-board storage and data processing systems (Davis *et al.*, 2005). Alternative systems to VPR aimed to increase accuracy by allowing observations of zooplankton in greater biological detail in a larger volume of water. Some of these alternative systems include the Large Area Plankton Imaging System (LAPIS; Madin *et al.*, 2006), Underwater Vision Profiler (UVP; Gorsky *et al.*, 1992) and In Situ Ichthyoplankton Imaging System (ISIIS; Cowen & Guigand, 2008). Apart from the development of imaging hardware, software used for automated zooplankton identification and classification has also significantly improved during the past few decades (reviewed in Benfield *et al.*, 2007; Sieracki *et al.*, 2010).

Particle detection devices are a separate group of optical zooplankton observation systems that estimate the size of particles passing through an illumination field (Sprules, 1992). The earliest particle detection system, named the Electronic Zooplankton Counting Device (EZCD) estimated the size of the zooplankton by measuring the interference caused by particles crossing an electrical field (Boyd & Johnson, 1969). The use of illumination fields and photodetectors instead of electrical fields for particle detection began in the 1970s (Cooke *et al.*, 1970). The most prominent was the Optical Plankton Counter (OPC), which produces size distributions of zooplankton approximating to an equivalent spherical diameter (Herman, 1988, 1992). Sprules *et al.* (1998) experimented with the optimal beam length and developed calibration algorithms for using OPCs in quantitative zooplankton surveys in freshwater lakes, which were later implemented to assess zooplankton communities of the North American Great Lakes by Yurista, Kelly & Miller (2005). The second generation of OPCs named the Laser Optical Plankton Counter (LOPC; Herman, Beanlands & Phillips, 2004) was better suited for studying zooplankton distributions in turbid freshwater systems, given its ability to resolve high densities of smaller particles compared to OPCs (Finlay, Beisner & Barnett, 2007).

(3) Tracking and simulation methods

(*a*) Tracking vertical migrations of individuals

Since the mid-19th century, significant advances have been made to trace zooplankton vertical migrations in experimental enclosures using videography. Baylor (1959) introduced a method to videotape planktonic microcrustaceans illuminated with submerged infrared lights using infrared-sensitive video cameras (silhouette videography). This method was used in classic plankton tower experiments (Lampert & Loose, 1992) to analyse the diel vertical migration and swimming behaviour of *Daphnia* spp. by tracing individuals across time and two-dimensional space (Lampert, 1993; Dodson, Tollrian & Lampert, 1997; Winder, Spaak & Mooij, 2004). Infrared-based silhouette videography was also employed in the tracking of individual zooplankton in more recently

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

introduced miniature plankton columns (Maszczyk, 2016). As analysing individual trajectories is a time-consuming process that involves the stopping of the video playback at regular intervals and measuring the animal's position, automated zooplankton motion-analysing systems were developed in the 1980s (Buskey, 1984). These systems significantly improved the efficiency of individual tracking and allowed motion trajectories and swimming speeds to be monitored seamlessly in three dimensions. As a result, Ramacharan & Sprules (1989) used four mirrors simultaneously to project two orthogonal views of a plankton aquarium into a single infrared-sensitive video camera to obtain a three-dimensional perspective. Since zooplankton appeared on the videotape as bright spots on a dark background, their computer-based tracking system was instructed to trace these bright spots across space and time.

An alternative to infrared-based silhouette videography was recently developed by Lard *et al.* (2010). This method is based on a nano-labelling technique that involves the coating of zooplankton with commercially available nanometre-sized fluorescent probes (quantum dots), which do not affect the behaviour of the animals. Instead of infrared light, the scene is illuminated with blue light (excitation wavelength $\approx$ 465–495 nm), where the individuals are recorded and tracked using fluorescence-sensitive cameras. Ekvall *et al.* (2013) used this labelling technique to study the swimming behaviour of several freshwater zooplankton species. They used a dual camera system facing a cube-shaped aquarium at a 90° angle to monitor the zooplankton behaviour in three dimensions. In a recent study, Fernández *et al.* (2020) used the same quantum labelling and tracking technique to assess the morphological and behavioural responses of two *Daphnia pulex* populations against UV exposure. Here, in an aquarium with a surface flux of UV irradiance, the *D. pulex* population collected from a high-UV environment took refuge at its deeper end, while those collected from a low-UV environment developed photo-protective compounds and reduced the refuge-taking behaviour. Nanotechnology-based tracking of zooplankton is still in its infancy and there is a need to develop these methods for marine taxa. Although these tracking methods are currently limited to small aquaria (largely due to the limitations of the camera field of view), recently developed aquatic inelastic hyperspectral LiDAR (Light Detection and Ranging) profilers (Zhao *et al.*, 2016) offer great promise to conduct these experiments in larger experimental enclosures (Zhao *et al.*, 2018).

(*b*) Simulating vertical migrations of virtual individuals

Since the 1980s, Individual Based Models (IBMs) have provided a cost-effective alternative to simulate the vertical behaviour of virtual individuals in computer-generated model environments (reviewed in Carlotti, Giske & Werner, 2000; Everett *et al.*, 2017). As model environments can be easily manipulated, IBMs have become a useful tool for studying individual- and population-level responses of zooplankton to environmental variability. However, to maintain computational efficiency, the virtual individuals in IBMs are significantly simplified compared to real zooplankton. For example, Fiksen (2000) represented the individuals of the high-latitude marine copepod *Calanus finmarchicus* as entities with a body mass, energy reserve mass and grouped developmental stage (eggs, nauplii, and copepodites). Most IBMs simulate the entire life cycle of individuals, which includes growth and development, survival (e.g. starvation tolerance, vertical migration, energy storage, overwintering) and reproduction.

The simulation of vertical migrations in IBMs requires: (*i*) proxies to represent the timing and amplitude of the migration; (*ii*) an estimate of the vertical swimming velocity of individuals; and (*iii*) a mechanism for depth (vertical habitat) selection. Several proxies are used to represent the timing and amplitude of zooplankton vertical migrations in IBMs. DVM is usually represented by the photoreactive behaviour of individuals, which is learned during their lifespan in machine learning-driven behavioural models (e.g. Eiane & Parisi, 2001; Strand, Huse & Girske, 2002) or evolves across generations in optimisation-driven behavioural and life-history models (e.g. Giske *et al.*, 1997; Tarling *et al.*, 2000). The adoption of proxies to represent the timing and amplitude of SVM remains challenging, as little is known about its proximate drivers. Consequently, some models impose hard constraints to fix the timing of the seasonal ascents and descents to match empirical estimates. For example, the IBM for *Calanus finmarchicus* by Carlotti & Wolf (1998) was formulated such that the simulated population enters overwintering after day 210 (July 29) and exits overwintering after day 95 (April 5). Many other models allow the timing and amplitude of SVM to vary among individuals of the population by introducing evolvable parameters, which are optimised using evolutionary algorithms or stochastic dynamic programming (e.g. Fiksen, 1997, 2000; Bandara *et al.*, 2018; Huse *et al.*, 2018). The vertical swimming velocities and patterns simulated in IBMs are usually adopted from empirical estimates. For example, Ringelberg (1995*a*) developed a DVM model for *Daphnia*, which used trigonometric oscillatory functions to simulate their 'hop and sink' behaviour. The model simulations were comparable to the empirical patterns, since the periodicity of the modelled sine curve was adjusted to match those observed in experimental enclosures. By contrast, the recent model for high-latitude *Calanus* spp. by Bandara *et al.* (2019) adopted the 'cruising' behaviour of copepods and assumed a constant cruising velocity, which was allometrically scaled to replicate intra- and inter-individual variability based on the vertical migration velocities recorded using acoustic devices. Among the commonly used techniques for depth selection are random-walk algorithms (e.g. Schmitt & Seuront, 2001; Dupont *et al.*, 2009), position calculation and placement methods (e.g. Carlotti & Wolf, 1998; Bandara *et al.*, 2019) and vertical habitat-selection methods based on optimisation (e.g. Fiksen & Giske, 1995) or game theory approaches (e.g. Pinti & Visser, 2019).

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

V. CHALLENGES, OPPORTUNITIES AND DIRECTIONS FOR FUTURE RESEARCH

The present understanding of zooplankton vertical migrations is the outcome of a wealth of field investigations, laboratory experiments and modelling studies conducted over the past two centuries. The rapid ongoing methodological developments are placing us at an exciting time point in the development of research on vertical migrations and there are several avenues where much progress can still be made.

(1) Improving the quality of zooplankton vertical distribution data

(*a*) Strategies to improve data resolution

Zooplankton sampling methods (e.g. plankton nets, traps and pump systems) produce data with excellent biological resolution and allow the identity of migrations to be resolved to the individual and developmental-stage levels and the estimation of many individual attributes, such as body size, lipid levels, sex and respiration rates. However, sampling data come with coarse vertical spatial resolution, since traps and pumps work at prescribed depths and plankton nets are hauled along large vertical stretches of tens to hundreds of metres. Further, due to operational difficulties and laborious enumeration and identification processes involved in data processing, plankton sampling systems are not suited to produce data at higher temporal resolution. By contrast, acoustic observation systems, such as high-frequency echosounders, produce data with excellent vertical spatial and temporal resolution. However, acoustic devices lack the biological resolution to describe the species- and stage-specificity of vertical migrations. The best alternative is to use acoustic devices alongside zooplankton sampling devices or optical *in-situ* observation systems, which allows extensive groundtruthing of the data (Stanton *et al.*, 1994). For example, Kahn & Lavery (2019) used a broadband echosounder alongside a digital zooplankton imaging system to describe the summertime vertical dynamics of DSLs off the shelf break of New England. The three-dimensional holographic images collected by the imaging system were useful for verifying the biological characterisation of the acoustic data and also aided in cross-validating the sound-scattering models used to estimate zooplankton abundance and biomass. Zooplankton imaging systems, such as the VPR and its subsequent developments, are superior to acoustic devices in terms of biological resolution. Although the biological resolution of zooplankton imaging systems is not yet fully comparable to that produced by zooplankton sampling devices, significant improvements can be expected with the rapid advances in high-resolution camera hardware and development of state-of-the-art image-recognition algorithms.

(*b*) Strategies to improve data coverage

Although plankton nets provide excellent vertical spatial coverage down to thousands of metres of depth, they do not sample the near-bottom (hyperbenthic) zooplankton communities. Studies conducted using epibenthic samplers (reviewed in Wiebe & Benfield, 2003) have indicated that the hyperbenthic zone is used as a refuge during the DVM of many coastal ocean zooplankton (Koulouri *et al.*, 2009) and serves as a prominent overwintering habitat for high-latitude copepods (Auel *et al.*, 2003; Hirche *et al.*, 2006). Therefore, it is important to use sampling devices that are capable of covering the entire water column in zooplankton vertical migration studies. Further, since overwintering in deeper waters and diapause in sediments are common to both marine and freshwater zooplankton, sampling efforts should encompass both the water column and the sediment to study a broader spectrum of zooplankton seasonal vertical strategies.

Despite the use of horizontally or obliquely towed high-speed samplers to address the lack of horizontal spatial coverage of plankton nets, they yield little information about the vertical dimensionality of zooplankton migrations (i.e. they lack vertical spatial coverage). A cumbersome approach to solve this problem is simultaneously to use multiple high-speed sampling devices attached to the same towline at various depths (e.g. Miller, 1961; Swain & Roijackers, 1985). However, this requires a significant additional post-processing effort for the collected samples. The use of acoustic or optical *in-situ* observation devices on autonomous underwater vehicles (AUVs) or remotely operated underwater vehicles (ROVs) is a better alternative to collect zooplankton vertical distribution data with greater horizontal and vertical spatial coverage. These mobile operations are facilitated by the use of compact and power-efficient glider-class echosounders (e.g. Benoit-Bird *et al.*, 2018; Pedersen *et al.*, 2019), acoustic Doppler profilers (e.g. Baumgartner & Fratantoni, 2008; Powell & Ohman, 2012), digital imaging systems (Guo *et al.*, 2018; Ohman *et al.*, 2019) and optical plankton counters (e.g. Pedersen *et al.*, 2010; Ohman *et al.*, 2013), which provide three-dimensional spatial coverage of zooplankton distributions.

Compared to high-speed samplers and AUV-mounted *in-situ* observation systems, airborne (e.g. Churnside & Thorne, 2005) and spaceborne (e.g. Winker *et al.*, 2009) LiDAR provides unprecedented horizontal spatial coverage of the upper ocean vertical migrants (Hostetler *et al.*, 2018). For example, Behrenfeld *et al.* (2019) used the backscattering signals of neodymium-doped yttrium aluminium garnet lasers (Nd:YAG) measured onboard the Cloud Aerosol LiDAR and Infrared Pathfinder Satellite (CALIPSO) and observed pronounced DVM patterns in subtropical gyres, which are usually associated with clearer waters. However, the identity of these migrants and the proximate drivers of their DVM remained unclear given the poor biological resolution in LiDAR data and due to the lack of regional- and global-scale zooplankton sampling or observation data for groundtruthing. The availability of spaceborne LiDAR data with global coverage should encourage modellers to develop broader spatial-scale generalised DVM models, because these data can be used for model validation.

Another advantage of spaceborne remote observation is that it provides data with unprecedented temporal coverage. For example, Behrenfeld *et al.* (2019) compiled a 20-year

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

timeseries of the above CALIPSO Nd:YAG laser backscattering data and used it to derive correlations between the estimated DVM biomass and pelagic primary production. Many marine observatories keep consistent long-term records of zooplankton net data in different parts of the world's oceans. The National Oceanic and Atmospheric Administration's coastal and oceanic plankton ecology production and observation database lists many such marine zooplankton timeseries (https://www.st.nmfs.noaa.gov/copepod/metabase/). Similar long-term collections of freshwater zooplankton data also exist and are listed in the Freshwater Information Platform's freshwater biodiversity data portal (http://data.freshwaterbiodiversity.eu/). Since many of these data sets are freely accessible, they should be used to study the interannual and decadal variations of zooplankton vertical migrations and their environmental correlates. Moored and vessel-mounted acoustic devices, such as Acoustic Doppler Current Profilers (ADCPs) are also used to generate long-term *in-situ* observations of zooplankton vertical distributions. The Western North Atlantic and Pacific ADCP data sets are listed in the NOAA Joint Archive of Shipboard ADCP (https://uhslc.soest.hawaii.edu/sadcp/). Although FerryBoxes (instrumental assemblages attached to commercial and routine maritime patrol vessels) are becoming increasingly popular for surface-ocean environmental monitoring in the Eastern North Atlantic (Petersen *et al.*, 2003; Ainsworth, 2008; Petersen, 2014), zooplankton profilers are not yet used as standard in these instrument packages. As a cost-effective means of generating long-term zooplankton vertical distribution data, the feasibility of including high-frequency echosounders, ADCPs or relatively inexpensive inelastic hyperspectral LiDAR profilers (Zhao *et al.*, 2016) in FerryBox systems should be evaluated. Advances in power management, under-ice communication, obstacle avoidance and navigation systems (e.g. Jones, Morozov & Manley, 2013; Freitag *et al.*, 2015) should be used to expand AUV operations into polar regions, where *in-situ* year-round zooplankton vertical distribution data are rare.

As zooplankton vertical migrations are often linked to the dynamics of the food and predation environments, data covering multiple trophic levels are required to generate a broader understanding of their causes and consequences. However, improvement of biological coverage of data is challenging, as sampling, observation or tracking devices usually focus on a narrow range of lifeforms and sizes. The best alternative is the combined use of zooplankton monitoring techniques in community-wide zooplankton vertical migration studies. A common approach used in marine meso- and macrozooplankton studies is to combine several nets, such as WP-2 and WP-3, with intermittent pelagic trawls to capture planktivorous fish (Skjoldal *et al.*, 2013). In freshwater systems, plankton nets are used alongside traps and pump samplers (Masson *et al.*, 2004). The use of multifrequency echosounders for zooplankton and fish monitoring is an elegant way to reduce the laborious post-processing of zooplankton samples. However, none of these techniques are well suited to monitor megaplanktivores (e.g. filter-feeding sharks, rays and whales), who, although not numerous, can have a significant predatory impact on zooplankton populations (Kenney *et al.*, 1986; Armstrong *et al.*, 2016). Therefore, future community-wide zooplankton vertical migration studies should use techniques such as pop-up archival tagging for monitoring non-sound-producing megaplanktivores (e.g. filter-feeding sharks; Sims *et al.*, 2003) and passive acoustics, such as hydrophone arrays to identify and track sound-producing megaplanktivores (e.g. cetaceans; Giraudet & Glotin, 2006).

Environmental DNA (eDNA) approaches (Ogram, Sayler & Barkay, 1987) provide a possible alternative to simultaneous monitoring of multiple trophic levels in community-wide vertical migration studies. This involves the use of next-generation sequencing (NGS) technologies for mass DNA sequencing and concurrent molecular identification of multiple taxa in water samples (Shokralla *et al.*, 2012; Taberlet *et al.*, 2012). Due to the rapid degradation of eDNA, it is suitable to identify shorter-term pelagic occurrences of lifeforms (e.g. planktivorous fish) and make rough estimations of their abundances (Lacoursière-Roussel, Rosabal & Bernatchez, 2016; Stoeckle, Soboleva & Charlop-Powers, 2017). However, further studies are required to test if an eDNA approach could be effective in the vertical characterisation of lifeforms.

(2) The need to broaden SVM research

Compared to DVM, SVM is a relatively understudied behaviour. Although many studies directly focus on overwintering and diapause, the related seasonal vertical movements are often taken for granted. However, SVM possesses notable community-wide implications and contributes significantly to the buffering of human-mediated global climate change (Baumgartner & Tarrant, 2017; Record *et al.*, 2018). One particular area that needs priority is research on the control mechanisms underlying diapause termination and seasonal ascent of high-latitude zooplankton. This knowledge holds the key to understanding the 'unexpected' levels of wintertime activity of herbivorous zooplankton recently observed during the polar night (reviewed in Berge *et al.*, 2020). For example, Bandara *et al.* (2016) found that *Calanus* spp. occupying a high-Arctic sill fjord gradually ascended from overwintering depths from late-November onwards and most of the population was in the upper 50 m by mid-February – *ca.* 5 months ahead of the onset of pelagic primary production. Recent findings point to elevated invertebrate predation at overwintering depths (Błachowiak-Samołyk *et al.*, 2015), energy resource exhaustion and starvation (Daase *et al.*, 2013*b*), and availability of alternative food sources (Hobbs *et al.*, 2020) as potential drivers of these mid-winter ascents. However, further studies are needed to develop a better understanding of the proximate drivers and the adaptive significance of these migrations and the dark-season survival strategies of high-latitude zooplankton.

The biggest challenge to studying the diapause termination and seasonal ascent of high-latitude zooplankton is the logistics of sampling zooplankton populations during the

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

winter-to-spring transition, when the ascent migrations usually occur. In addition, there are obvious difficulties involved with conducting proper experimental studies of SVM. For example, unlike most freshwater zooplankton (e.g. *Daphnia* spp.), it is difficult to induce and terminate diapause among marine zooplankton under laboratory conditions (Hirche, 1996*a*). Further, data with individual-level resolution will be needed to understand proximate drivers and adaptive value fully, as state-dependent responses are common (Hays *et al.*, 2001) and key states, such as lipid reserves should ideally be measured at the level of individuals (Vogedes *et al.*, 2010) and not from pooled samples. Addressing these challenges will involve devoting more effort towards sampling or observing zooplankton populations and the individual variability within them (Varpe, 2012), and relating their vertical distributions to environmental variables. In this regard, environmental variables should be tested for combined influence, as the phenology of diapause induction and termination can be altered when variables such as irradiance, temperature, food availability and predation risk operate in concert (Walsh, 2013; Bandara *et al.*, 2019). Studying SVMs in marine environments with higher advective potential is a challenging task. This is due to the impact of advection on zooplankton recruitment and the difficulties it offers when interpreting vertical changes of zooplankton abundance over time purely as a behavioural (active) process (Pearre, 1979). To minimise the advective influence, SVM studies conducted in semi-isolated marine environments, such as bays, sill fjords and lochs (Kosobokova, 1999; Clark *et al.*, 2012; Bandara *et al.*, 2016) should be encouraged.

(3) The importance of studying DVM and SVM in concert

As most zooplankton vertical migration studies either focus on DVM or SVM, the present understanding of the interactions between these two migrations remains limited. The combined influence of DVM and SVM on the fitness and phenology of zooplankton has been a focus of some studies (e.g. Loose & Dawidowicz, 1994; Fiksen, 1997; Fiksen & Carlotti, 1998). In the recent unidimensional high-resolution models of Bandara *et al.* (2018, 2019), DVM of high-latitude calanoid copepods emerged as an immediate response to elevated visual predation risk. This reduced the growth rates of the modelled copepods as they had periodically to abandon food-rich near-surface waters (see also Houston, McNamara & Hutchinson, 1993). Consequently, the predicted seasonal descent and overwintering occurred with a significant delay at higher visual predation risk, since the DVM-induced reduction in growth rate yielded more time for the copepods to develop to a late-juvenile stage (CIII, CIV or CV) with sufficient reserves. These novel findings should be tested further in refined models and validated against field data before being generalised.

The modification of behavioural and life-history strategies in response to environmental variability can have a feedback effect on the spatial distribution of zooplankton (McManus & Woodson, 2012). For example, predation-induced changes of diel and seasonal vertical behaviour (i.e. changes in the timing and amplitude of DVM and SVM) can drive zooplankton across differential water masses, which may eventually lead to advective or retentive processes. Since the extent of zooplankton vertical behaviour is strongly related to their body size and developmental stage, a size- and stage-specific variability can also be predicted in the expected advective or retentive feedback. For example, individual based Lagrangian simulation models have shown that diel vertical migrants possess a better chance of retention within the productive nearshore upwelling regions, since the typical night-time offshore surface drift brought about by Ekman transport is compensated by the daytime descent to sub-surface shoreward-moving currents (Batchelder, Edwards & Powell, 2002, Marta-Almeida *et al.*, 2006). Nonetheless, since younger developmental stages do not usually have the capability to perform high-amplitude DVM, a net offshore movement of the zooplankton population is expected over time. These offshore-advected older developmental stages overwinter off the shelf breaks, and ascend to shoreward moving subsurface upwelling currents in the following year (Peterson *et al.*, 1979). Maps *et al.* (2011) used a three-dimensional physical circulation model of the Gulf of St. Lawrence to drive a unidimensional behavioural and life-history simulation model of the high-latitude copepod *Calanus finmarchicus* and found that the timing and amplitude of DVM and SVM are crucial for their retention within the study area. However, whether similar DVM–SVM interactions exist in high-latitude coastal marine environments, which are influenced by substantial variations of tidal regimes and cross-shelf exchange of water masses is not well known.

One possible reason why DVM–SVM interactions are less studied in high-latitude systems is the argument that there is no pronounced (synchronised) DVM during most of the year. The absence of DVM during much of the high-latitude productive season (particularly in summer) is often discussed in relation to the lack of 'perceivable' diurnal variations of irradiance (Buchanan & Haney, 1980; Błachowiak-Samołyk *et al.*, 2006; Cottier *et al.*, 2006). However, although not necessarily perceivable to the human eye, diurnal variations of irradiance occur during the high-latitude summer (the period of midnight sun), which are detectable by instruments and perhaps by zooplankton. Further, recent studies show that several species of Arctic copepods and krill are highly sensitive to light (with lower detection thresholds $\sim 10^{-8}$ μmol photons m^{-2} s^{-1}) and perform DVMs during the high-Arctic winter (polar night) using moonlight, starlight and light from aurorae as proximate cues (Båtnes *et al.*, 2015; Cohen *et al.*, 2015; Last *et al.*, 2016). This indicates that diurnal variations of summertime irradiance should be a sufficient visual cue for these highly light-sensitive zooplankton. The prevalence of high-latitude summertime DVM under the threat of visual predation hints that the absence of DVM in certain studies may be due to the absence of planktivorous fish (as demonstrated in some lower-Arctic settings; e.g. Fortier

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

et al., 2001) or due to alterations of the underwater light climate following the loss of sea ice (Wallace *et al.*, 2010). As more planktivorous fish are expected to migrate poleward due to oceanic climate shifts (Perry *et al.*, 2005) and experience more light in the water column as sea ice melts (Langbehn & Varpe, 2017), DVM at higher latitudes will become more pronounced (e.g. lesser near-surface foraging time and greater migration amplitude) and, therefore, DVM–SVM interactions deserve significant attention.

A challenge to study DVM and SVM in concert is that they occur over contrasting spatial and temporal scales. Field campaigns (e.g. shipboard sampling) seldom last for more than a few weeks at higher latitudes and are usually conducted in the ice-free periods of the year due to logistic challenges. Moreover, experimental enclosures cannot accurately reproduce abiotic and biotic environmental dynamics (e.g. predation risk, bottom depth) encountered in nature, especially in the marine realm. Although mechanistic simulation models appear to be a cost-effective alternative to address these problems, most high-latitude zooplankton life-history and biogeography models tend to disregard shorter-term diel vertical behaviour due to the elevated computational demands of simulating higher biological detail in shorter time steps. Therefore, modellers should aim to utilise emerging computer hardware [e.g. advanced central, graphical and neural processing units (CPUs, GPUs and NPUs)] and methods such as high-performance computing (e.g. Džeroski, 2001; Owens *et al.*, 2008) and artificial intelligence (e.g. Huse, Strand & Giske, 1999; Eiane & Parisi, 2001) to improve the computational efficiency of mechanistic simulation models.

(4) Vertical migration and climate change

Many animal migrations are expected to change due to climate warming and related environmental change (Cotton, 2003; Wilcove & Wikelski, 2008; Bauer & Hoye, 2014). It is largely unknown how zooplankton vertical migrations are responding to climate change, but some studies provide insights. Work conducted in lentic freshwater systems indicate that increased summertime surface temperatures and UV irradiance will hinder the entry of cladoceran zooplankton to the epilimnion and thus reduce the amplitude of their DVM (De Stasio *et al.*, 1996; Snucins & John, 2000; Cooke *et al.*, 2008). Nonetheless, further studies are required to test if starvation effects and predation pressure can alter these patterns. In shallow freshwater systems, temperature increases can be expected throughout the water column, which can drive changes in SVM timing as hatching phenology of resting eggs is altered (Chen & Folt, 1996). However, temperature effects will not be pronounced in systems where photoperiod acts as the primary cue for the hatching of resting eggs (Winder & Schindler, 2004). Some studies conducted in temperate freshwater lakes suggest that SVM of planktonic inhabitants will gradually diminish in response to climate change. For example, according to Tsugeki, Ishida & Urabe (2009), wintertime upper pelagial temperatures of Lake Biwa (Japan) increased gradually from the mid-1960s to early 2000s, causing primary production to continue more or less year-round (which did not occur in the winter months prior to the warming). Due to the year-round food supply, the resting egg production, diapause and SVM of herbivorous zooplankton (e.g. *Daphnia galeata*) gradually diminished over the years as they could occupy the upper pelagial year-round.

In the marine realm, climate-related changes in vertical migrations should be particularly pronounced in high-latitude systems due to the predicted increase of upper ocean temperatures, loss of sea ice cover (and improved underwater light regime), elevated primary production and poleward migration of pelagic planktivores (Meredith *et al.*, 2019). Although research is scarce, several testable predictions can be made. First, the extent of DVM can be expected to increase in the future, especially among the herbivore zooplankton community due to elevated food availability and increased visual predation risk. However, the effects of ambient temperature and size-dependent visual predation risk on the body size of zooplankton should also be considered in predicting climate change influences of DVM, since zooplankton vertical behaviour is proportional to their body size (Ohman & Romagnan, 2016). Similarly, changes in turbidity, for instance caused by more run-off from land, will complicate these processes and possibly lead to less DVM and altered zooplankton phenology. Second, the timing of SVM will also shift in future high-latitude oceanic environments due to the predicted earlier onset and longer duration of pelagic primary production (Sydeman & Bograd, 2009) – but note that the seasonal primary production may occur later in some seas (Opdal, Lindemann & Aksnes, 2019). However, an assessment of predation risk is required to make accurate predictions about the extent and direction of shifts in SVM timing. Third, the predicted climate-related warming of the deeper pelagial will lead to faster catabolisation of stored lipids and thus shorten the overwintering duration of high-latitude zooplankton (Saumweber & Durbin, 2006; Wilson *et al.*, 2016). The failure to prolong overwintering duration until the onset of the following productive season could be catastrophic for many herbivorous zooplankton populations, particularly if the animals cannot survive on alternative food sources in the absence of their primary food source (phytoplankton). However, whether the warming of the deeper pelagial will drive changes in the vertical habitat selection of zooplankton remains unclear.

If climate change-related future DVM and SVM shifts become pronounced, it will likely have significant impacts on the ocean's biologically driven carbon sequestration. In a recent mini-synthesis, Brierley (2014) hypothesised that increased DVM in a future ocean will enhance the carbon pump. He wrote: "*More primary production will support more grazing zooplankton, which will undertake more vertically extensive diel migrations to avoid the better-illuminated surface zone. This will transport fixed carbon deeper into the ocean interior, removing it from the atmosphere for longer in a climatically beneficial negative feedback loop*" (Brierley, 2014, p. 1076). Both supporting and opposing

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

evidence exist in this regard. For example, Behrenfeld *et al.* (2019) analysed a *ca.* 20-year DVM timeseries and found a temporal increase in DVM biomass in highly productive subtropical marine realms and a decrease in the North Atlantic. These findings were corroborated by a 55-year timeseries study conducted in the North Atlantic by Brun *et al.* (2019). Accordingly, the vertical carbon flux driven by zooplankton DVM, SVM and faecal pellet production decreased in the North Atlantic since the 1960s, except for the north-western boundary of the study area. According to the authors, these changes largely underpin the climate-related spatio-temporal changes in vertical migration biomass. An emerging hypothesis is that climate-related warming of the upper ocean will favour the proliferation of smaller zooplankton, while larger taxa will be numerically diminished or redistributed further north (Arctic) or south (Antarctic) (Chust *et al.*, 2014; Mäkinen, Vuorinen & Hänninen, 2017; Møller & Nielsen, 2020). Whether the predicted future climate trends will enhance the vertical migration contribution to the biological pump thus hinges on the ability of a larger number of smaller-bodied zooplankton taxa to compensate the carbon flux effects of fewer larger-bodied taxa. Further research is needed to obtain a better understanding of these complex trade-offs and feedbacks.

In coastal regions where vertical migrations may aid as retentive or advective facilitatory mechanisms, climate change-related shifts of DVM and SVM may lead to alterations of geographic distributions of zooplankton (Heath *et al.*, 1999). This is one of the least addressed areas of research, where the predictive potential of mechanistic simulation modelling approaches can be harnessed. One particular approach is to couple a unidimensional species-specific behavioural and life-history simulation model (biological model) to a three-dimensional ocean circulation model (physical model) of the region of interest. Usually, these coupled models work in a way that the physical model simulates the circulation patterns for a selected calendar year and the biological model runs for multiple annual iterations over the simulated physical environment until some stabilisation criterion is met (e.g. Huse *et al.*, 2018). What has not been widely attempted to date is to use a climate model to alter the environmental forcing of the physical model and establish a time series into the future (e.g. from present day to the year 2100 using IPCC predictions). The biological model can be executed over this timeseries (rather than iterating over the same annual circuit) and the modeller can investigate the extent to which climate change-related changes of DVM and SVM influence the geographic distribution of the modelled zooplankton species.

(5) From genes to ecosystems: the importance of integrated and collaborative approaches

As for any animal migration, zooplankton vertical migration is not a population attribute but is a collection of behavioural decisions made by individual zooplankton (Zink, 2002). Since most zooplankton are relatively small and seldom exceed a few millimetres in size, their behavioural decisions and position in the water column can be sensitive to fine-scale variations of the environment. Therefore, future research should emphasise the role of individual variability in making diel and seasonal habitat choice decisions (Kralj-Fišer & Schuett, 2014). Further, since individual motivations for behavioural decisions may be rooted in the genetic material (Häfker *et al.*, 2017), molecular genetic studies should be prioritised to formulate a comprehensive theory on the proximate control of zooplankton vertical migrations. There is also a growing need to explore the community and ecosystem consequences of vertical migrations, both under present and future environmental contexts, as vertical migrations are connected across trophic levels through predator–prey interactions (Bollens *et al.*, 2010) including complex game-type interactions (Pinti & Visser, 2019) and perform a crucial role in the buffering of human-mediated global climate change (Brierley, 2014; Record *et al.*, 2018).

Studying a behaviour with such broad ecological, evolutionary and economic consequences not only requires the integration of various classic and state-of-the-art zooplankton vertical migration study techniques (as discussed in previous sections) but also warrants interdisciplinary research involving animal physiology and biochemistry, marine and evolutionary ecology, behaviour, molecular genetics, mathematical modelling, hydrography and climatology. Collaborations and comparisons across disciplines are also likely to facilitate advances, such as comparing terrestrial and aquatic arthropods (Varpe & Ejsmond, 2018*a*). Further, collaborative efforts across marine and freshwater realms could also contribute significantly to improving the zooplankton vertical migration knowledgebase. For example, behavioural and life-history patterns of the freshwater cladoceran *Daphnia* have been studied extensively over the past two centuries, and consequently, it is now considered a 'model system' to improve the mechanistic understanding of the interplay between various traits at the levels of genes, individuals and populations and its consequences for community and ecosystem dynamics (Miner *et al.*, 2012). The myriad experiments conducted on the proximate cues of DVM and diapause (with respect to resting eggs) of daphniids should be studied by marine planktologists to shed new light on the cues for overwintering entry and exit and SVM of marine zooplankton, especially with respect to the presence of predators where research is still largely model- and theory-driven but with limited empirical data. On the other hand, advances in marine research could contribute to exploring under-visited avenues in freshwater systems. One particular area that may benefit in this regard is the duality of freshwater zooplankton diapause systems, which can switch between the production of resting eggs and overwintering in advanced developmental stages (Block, 2017). Methodological developments regarding sampling, observing and quantifying overwintering strategies of marine zooplankton, especially involving high-frequency acoustics, should be adopted in freshwater systems. We envisage considerable pay-offs from more integrative approaches to research on zooplankton migrations.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

VI. CONCLUSIONS

(1) Research on zooplankton migrations has developed as a continuous process of mainly curiosity-driven work with 200 years of history and scientific developments characterised by important and considerable descriptions of diversity as well as theoretical and mechanistic understanding.
(2) The DVM knowledgebase is broad and its causes and consequences are well studied in both marine and freshwater systems. Comparatively, our understanding of SVMs is more limited, and studies of the interactions between the two timescales and forms of migrations are largely lacking.
(3) While SVM research should be encouraged, a generic emphasis is needed to improve current zooplankton sampling, observation, tracking and simulation techniques towards producing vertical distribution data with better spatial, temporal and biological resolution and coverage, including more and better individual-level observations and measurements.
(4) Key focal points for future research include DVM–SVM interactions, climate change implications on vertical migrations and integrative approaches combining rapid developments within many fields from genetics to ecosystem science. Collaborative research across multiple disciplines is likely to lead to new and important findings about zooplankton migrations: the greatest synchronised animal movement of our planet.

VII. ACKNOWLEDGEMENTS

This work was funded by VISTA, a basic research program in collaboration between The Norwegian Academy of Science and Letters, and Statoil™ and by the project GLIDER, unmanned ocean vehicles, a flexible and cost-efficient offshore monitoring and data-management approach project (No. 269188/E30). L.W. received funding from the German Academic Exchange Service (DAAD, grant no. 91690872) during this work. We are grateful to the three reviewers for critically reading earlier drafts and suggesting substantial improvements. We also thank the Associate Editor, Dr Alison Cooper for suggesting necessary changes towards further improving the text.

VIII. REFERENCES

Aarflot, J. M., Aksnes, D. L., Opdal, A. F., Skjoldal, H. R. & Fiksen, Ø. (2019). Caught in broad daylight: topographic constraints of zooplankton depth distributions. *Limnology and Oceanography* **64**, 849–859.

Aidley, D. (1981). Questions about migration. In *Animal Migration* (ed. D. Aidley), pp. 1–9. Press Syndicae of the University of Cambridge, New York.

Ainsworth, C. (2008). FerryBoxes begin to make waves. *Science* **322**, 1627–1629.

Aita, M. N., Yamanaka, Y. & Kishi, M. J. (2003). Effects of ontogenetic vertical migration of zooplankton on annual primary production–using NEMURO embedded in a general circulation model. *Fisheries Oceanography* **12**, 284–290.

Alcaraz, M. & Strickler, J. R. (1988). Locomotion in copepods: pattern of movements and energetics of *Cyclops*. *Hydrobiologia* **167**, 409–414.

Alldredge, A. & King, J. M. (1980). Effects of moonlight on the vertical migration patterns of demersal zooplankton. *Journal of Experimental Marine Biology and Ecology* **44**, 133–156.

Alldredge, A., Robison, B., Fleminger, A., Torres, J., King, J. & Hamner, W. (1984). Direct sampling and in situ observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. *Marine Biology* **80**, 75–81.

Allen, M. R. (2007). Measuring and modeling dispersal of adult zooplankton. *Oecologia* **153**, 135–143.

Alonso, C., Rocco, V., Barriga, J. P., Battini, M. Á. & Zagarese, H. (2004). Surface avoidance by freshwater zooplankton: field evidence on the role of ultraviolet radiation. *Limnology and Oceanography* **49**, 225–232.

Andersen, V. & Nival, P. (1991). A model of the diel vertical migration of zooplankton based on euphausiids. *Journal of Marine Research* **49**, 153–175.

Anderson, D. & Stolzenbach, K. (1985). Selective retention of two dinoflagellates in a well-mixed estuarine embayment: the importance of diel vertical migration and surface avoidance. *Marine Ecology Progress Series* **25**, 39–50.

Andrewartha, H. (1952). Diapause in relation to the ecology of insects. *Biological Reviews* **27**, 50–107.

Antsulevich, A. & Välipakka, P. (2000). *Cercopagis pengoi*—new important food object of the Baltic herring in the Gulf of Finland. *International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology* **85**, 609–619.

Aoki, K., Amano, M., Yoshioka, M., Mori, K., Tokuda, D. & Miyazaki, N. (2007). Diel diving behavior of sperm whales off Japan. *Marine Ecology Progress Series* **349**, 277–287.

Appel, D. S., Gerrish, G. A., Fisher, E. J. & Fritts, M. W. (2020). Zooplankton sampling in large riverine systems: a gear comparison. *River Research and Applications* **36**, 102–114.

Armstrong, A. O., Armstrong, A. J., Jaine, F. R., Couturier, L. I., Fiora, K., Uribe-Palomino, J., Weeks, S. J., Townsend, K. A., Bennett, M. B. & Richardson, A. J. (2016). Prey density threshold and tidal influence on reef manta ray foraging at an aggregation site on the great barrier reef. *PLoS One* **11**, e0153393.

Arnkværn, G., Daase, M. & Eiane, K. (2005). Dynamics of coexisting *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* populations in a high-Arctic fjord. *Polar Biology* **28**, 528–538.

Aruda, A. M., Baumgartner, M. F., Reitzel, A. M. & Tarrant, A. M. (2011). Heat shock protein expression during stress and diapause in the marine copepod *Calanus finmarchicus*. *Journal of Insect Physiology* **57**, 665–675.

Astthorsson, O. S. & Gislason, A. (2003). Seasonal variations in abundance, development and vertical distribution of *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis* in the East Icelandic Current. *Journal of Plankton Research* **25**, 843–854.

Atkinson, A. (1998). Life cycle strategies of epipelagic copepods in the Southern Ocean. *Journal of Marine Systems* **15**, 289–311.

Auel, H., Klages, M. & Werner, I. (2003). Respiration and lipid content of the Arctic copepod *Calanus hyperboreus* overwintering 1 m above the seafloor at 2,300 m water depth in the Fram Strait. *Marine Biology* **143**, 275–282.

Auel, H. & Verheye, H. M. (2007). Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela current upwelling system and the Angola–Benguela front. *Journal of Experimental Marine Biology and Ecology* **352**, 234–243.

Backus, R. H. & Barnes, H. (1957). Television-echo sounder observations of midwater sound scatteres. *Deep Sea Research* **4**, 116–119.

Bagøien, E., Kaartvedt, S., Aksnes, D. L. & Eiane, K. (2001). Vertical distribution and mortality of overwintering *Calanus*. *Limnology and Oceanography* **46**, 1494–1510.

Bagøien, E., Kaartvedt, S. & Øverås, S. (2000). Seasonal vertical migrations of *Calanus* spp. in Oslofjorden. *Sarsia* **85**, 299–311.

Baird, R. W., Hanson, M. B. & Dill, L. M. (2005). Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. *Canadian Journal of Zoology* **83**, 257–267.

Baird, R. W., Ligon, A. D., Hooker, S. K. & Gorgone, A. M. (2001). Subsurface and nighttime behaviour of pantropical spotted dolphins in Hawai'i. *Canadian Journal of Zoology* **79**, 988–996.

Baird, R. W., Webster, D. L., Schorr, G. S., McSweeney, D. J. & Barlow, J. (2008). Diel variation in beaked whale diving behavior. *Marine Mammal Science* **24**, 630–642.

Baird, W. (1850). *Natural History of the British Entomostraca*. Ray Society, London.

Ban, S. & Minoda, T. (1994). Induction of diapause egg production in *Eurytemora affinis* by their own metabolites. *Hydrobiologia* **292**, 185–189.

Bandara, K., Varpe, Ø., Ji, R. & Eiane, K. (2018). A high-resolution modeling study on diel and seasonal vertical migrations of high-latitude copepods. *Ecological Modelling* **368**, 357–376.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Bandara, K., Varpe, Ø., Ji, R. & Eiane, K. (2019). Artificial evolution of behavioral and life history strategies of high-latitude copepods in response to bottom-up and top-down selection pressures. *Progress in Oceanography* **173**, 134–164.

Bandara, K., Varpe, Ø., Søreide, J. E., Wallenschus, J., Berge, J. & Eiane, K. (2016). Seasonal vertical strategies in a high-Arctic coastal zooplankton community. *Marine Ecology Progress Series* **555**, 49–64.

Banse, K. (1964). On the vertical distribution of zooplankton in the sea. *Progress in Oceanography* **2**(supplement C), 53–125.

Barber, R. & Smith, R. L. (1981). Coastal upwelling ecosystems. In *Analysis of Marine Ecosystems* (ed. A. R. Longhurst), pp. 31–68. Academic Press, New York.

Batchelder, H. P., Edwards, C. A. & Powell, T. M. (2002). Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. *Progress in Oceanography* **53**, 307–333.

Båtnes, A. S., Miljeteig, C., Berge, J., Greenacre, M. & Johnsen, G. H. (2015). Quantifying the light sensitivity of *Calanus* spp. during the polar night: potential for orchestrated migrations conducted by ambient light from the sun, moon, or aurora borealis? *Polar Biology* **38**, 51–65.

Bauer, S. & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552.

Baumgartner, M. F. & Fratantoni, D. M. (2008). Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders. *Limnology and Oceanography* **53**, 2197–2209.

Baumgartner, M. F., Lysiak, N. S., Schuman, C., Urban-Rich, J. & Wenzel, F. W. (2011). Diel vertical migration behavior of *Calanus finmarchicus* and its influence on right and sei whale occurrence. *Marine Ecology Progress Series* **423**, 167–184.

Baumgartner, M. F. & Tarrant, A. M. (2017). The physiology and ecology of diapause in marine copepods. *Annual Review of Marine Science* **9**, 387–411.

Baylor, E. R. (1959). Infra-red observation and cinematography of Microcrustacea. *Limnology and Oceanography* **5**, 497–498.

Bayly, I. (1963). Reversed diurnal vertical migration of planktonic Crustacea in inland waters of low hydrogen ion concentration. *Nature* **200**, 704–705.

Bé, A. W. (1962). Quantitative multiple opening-and-closing plankton samplers. *Deep Sea Research and Oceanographic Abstracts* **9**, 144–151.

Bé, A. W., Ewing, M. & Linton, L. W. (1959). A quantitative multiple opening-and-closing plankton sampler for vertical towing. *ICES Journal of Marine Science* **25**, 36–46.

Beamish, F. W. H. (1966). Vertical migration by Demersal fish in the Northwest Atlantic. *Journal of the Fisheries Research Board of Canada* **23**, 109–139.

Behm, A. (1921). Das Behm-Echolot. *Annalen der Hydrographie und Maritimen Meteorologie* **49**, 241–247.

Behrenfeld, M. J., Gaube, P., Della Penna, A., O'Malley, R. T., Burt, W. J., Hu, Y., Bontempi, P. S., Steinberg, D. K., Boss, E. S., Siegel, D. A., Hostetler, C. A., Tortell, P. D. & Doney, S. C. (2019). Global satellite-observed daily vertical migrations of ocean animals. *Nature* **576**, 257–261.

Beklioglu, M., Gozen, A. G., Yildirim, F., Zorlu, P. & Onde, S. (2008). Impact of food concentration on diel vertical migration behaviour of *Daphnia pulex* under fish predation risk. *Hydrobiologia* **614**, 321–327.

Beklioglu, M., Telli, M. & Gozen, A. G. (2006). Fish and mucus-dwelling bacteria interact to produce a kairomone that induces diel vertical migration in *Daphnia*. *Freshwater Biology* **51**, 2200–2206.

Belk, D. (1970). Functions of the conchostracan egg shell. *Crustaceana* **19**, 105–106.

Benfield, M. C., Grosjean, P., Culverhouse, P. F., Irigoien, X., Sieracki, M. E., Lopez-Urrutia, A., Dam, H. G., Hu, Q., Davis, C. S. & Hansen, A. (2007). RAPID: research on automated plankton identification. *Oceanography* **20**, 172–187.

Benoit-Bird, K., Au, W. W. & Wisdoma, D. W. (2009). Nocturnal light and lunar cycle effects on diel migration of micronekton. *Limnology and Oceanography* **54**, 1789–1800.

Benoit-Bird, K., Patrick Welch, T., Waluk, C., Barth, J., Wangen, I., McGill, P., Okuda, C., Hollinger, G., Sato, M. & McCammon, S. (2018). Equipping an underwater glider with a new echosounder to explore ocean ecosystems. *Limnology and Oceanography: Methods* **16**, 734–749.

Berge, J., Cottier, F. R., Last, K. S., Varpe, Ø., Leu, E., Søreide, J. E., Eiane, K., Falk-Petersen, S., Willis, K. & Nygård, H. (2009). Diel vertical migration of Arctic zooplankton during the polar night. *Biology Letters* **5**, 69–72.

Berge, J., Cottier, F. R., Varpe, Ø., Renaud, P. E., Falk-Petersen, S., Kwasniewski, S., Griffiths, C., Søreide, J. E., Johnsen, G. H., Aubert, A., Bjærke, O., Hovinen, J., Jung-Madsen, S., Tveit, M. & Majaneva, S. (2014). Arctic complexity: a case study on diel vertical migration of zooplankton. *Journal of Plankton Research* **36**, 1279–1297.

Berge, J., Daase, M., Hobbs, L., Falk-Petersen, S., Darnis, G. & Søreide, J. E. (2020). Zooplankton in the polar night. In *Polar Night Marine Ecology: Life and Light in the Dead of Night* (eds J. Berge, G. Johnsen and J. H. Cohen), pp. 113–159. Springer International Publishing, Cham.

Berge, J., Varpe, Ø., Moline, M. A., Wold, A., Renaud, P. E., Daase, M. & Falk-Petersen, S. (2012). Retention of ice-associated amphipods: possible consequences for an ice-free Arctic Ocean. *Biology Letters* **8**, 1012–1015.

Berggraf, H. (1904). Apparat, hvormed havdybden kan måles, uden at apparatet har forbindelse med havbunden. *Teknisk Ukeblad* **22**, 404–411.

Bernot, R. J., Dodds, W. K., Quist, M. C. & Guy, C. S. (2006). Temperature and kairomone induced life history plasticity in coexisting *Daphnia*. *Aquatic Ecology* **40**, 361–372.

Bezerra-Neto, J. F. & Pinto-Coelho, R. M. (2007). Diel vertical migration of the copepod *Thermocyclops inversus* (Kiefer, 1936) in a tropical reservoir: the role of oxygen and the spatial overlap with *Chaoborus*. *Aquatic Ecology* **41**, 535–545.

Bhajan, W. & Hynes, H. (1972). Experimental study on the ecology of *Bosmina longirostris* (OF Müller)(Cladocera). *Crustaceana* **23**, 133–140.

Bianchi, D., Galbraith, E. D., Carozza, D. A., Mislan, K. & Stock, C. A. (2013). Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nature Geoscience* **6**, 545–548.

Bigelow, H. B. (1926). Plankton of the offshore waters of the Gulf of Maine. *Bulletin of United States Fisheries Beureau* **40**, 1–509.

Birge, E. (1882). Notes on Crustacea in Chicago water supply with remarks on the formation of the carapace. *Chicago Medical Journal and Examiner* **43**, 584–590.

Birge, E. (1904). The annual address of the president: the thermocline and its biological significance. *Transactions of the American Microscopical Society* **25**, 5–33.

Biscontin, A., Wallach, T., Sales, G., Grudziecki, A., Janke, L., Sartori, E., Bertolucci, C., Mazzotta, G., De Pittà, C., Meyer, B., Kramer, A. & Costa, R. (2017). Functional characterization of the circadian clock in the Antarctic krill, *Euphausia superba*. *Scientific Reports* **7**, 17742.

Błachowiak-Samołyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., Falk-Petersen, S. & Mouritsen, L. T. (2006). Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Marine Ecology Progress Series* **308**, 101–116.

Błachowiak-Samołyk, K., Wiktor, J. M., Hegseth, E. N., Wold, A., Falk-Petersen, S. & Kubiszyn, A. M. (2015). Winter Tales: the dark side of planktonic life. *Polar Biology* **38**, 23–36.

Blaustein, L. (1997). Non-consumptive effects of larval Salamandra on crustacean prey: can eggs detect predators? *Oecologia* **110**, 212–217.

Block, B. (2017). Hidden beneath the ice: actively overwintering zooplankton populations. *Duluth Journal of Undergraduate Biology* **4**, 1–11.

Block, B. A., Teo, S. L., Walli, A., Boustany, A., Stokesbury, M. J., Farwell, C. J., Weng, K. C., Dewar, H. & Williams, T. D. (2005). Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434**, 1121–1127.

Bollens, S. M. & Frost, B. W. (1989a). Predator-induced diet vertical migration in a planktonic copepod. *Journal of Plankton Research* **11**, 1047–1065.

Bollens, S. M. & Frost, B. W. (1989b). Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography* **34**, 1072–1083.

Bollens, S. M. & Frost, B. W. (1991). Diel vertical migration in zooplankton: rapid individual response to predators. *Journal of Plankton Research* **13**, 1359–1365.

Bollens, S. M., Frost, B. W. & Cordell, J. R. (1994). Chemical, mechanical and visual cues in the vertical migration behavior of the marine planktonic copepod *Acartia hudsonica*. *Journal of Plankton Research* **16**, 555–564.

Bollens, S. M., Quenette, J. A. & Rollwagen-Bollens, G. (2012). Predator-enhanced diel vertical migration in a planktonic dinoflagellate. *Marine Ecology Progress Series* **447**, 49–54.

Bollens, S. M., Rollwagen-Bollens, G., Quenette, J. A. & Bochdansky, A. B. (2010). Cascading migrations and implications for vertical fluxes in pelagic ecosystems. *Journal of Plankton Research* **33**, 349–355.

Bonacina, C. & Pasteris, A. (2001). Zooplankton of Lake Orta after liming: an eleven years study. *Journal of Limnology* **60**, 101–109.

Borcherding, J., Kiel, S., Struebig, A. & Arndt, H. (2017). Vertical migration of *Daphnia galeata* – evidence for the use of an alternative resource from a lethal environment. *Limnologica* **62**, 132–139.

Born, E. W., Teilmann, J., Acquarone, M. & Riget, F. F. (2004). Habitat use of ringed seals (*Phoca hispida*) in the north water area (North Baffin Bay). *Arctic* **57**, 129–142.

Bosch, H. & Taylor, R. R. (1973). Diurnal vertical migration of an estuarine cladoceran, *Podon polyphemoides*, in the Chesapeake Bay. *Marine Biology* **19**, 172–181.

Bowers, J. A. (1979). Zooplankton grazing in simulation models: the role of vertical migration. In *Perspectives on Lake Ecosystem Modeling* (eds D. Scavia and A. Robertson), pp. 53–73. Science, Ann Arbor.

Boyd, C. M. & Johnson, G. W. (1969). Studying zooplankton populations with an electronic zooplankton counting device and the LINC-8 computer. *Transactions of the Applications of Sea Going Computers* **83**, 83–90.

Bradford-Grieve, J., Nodder, S., Jillett, J., Currie, K. & Lassey, K. (2001). Potential contribution that the copepod *Neocalanus tonsus* makes to downward carbon flux in the Southern Ocean. *Journal of Plankton Research* **23**, 963–975.

Bratton, J. & Fryer, G. (1990). The distribution and ecology of *Chirocephalus diaphanus Prévost* (Branchiopoda: Anostraca) in Britain. *Journal of Natural History* **24**, 955–964.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Brendonck, L. & de Meester, L. (2003). Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia* **491**, 65–84.

Brendonck, L. & Riddoch, B. J. (1999). Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). *Biological Journal of the Linnean Society* **67**, 87–95.

Brierley, A. S. (2014). Diel vertical migration. *Current Biology* **24**, R1074–R1076.

Brierley, A. S. & Watkins, J. L. (2000). Effects of sea ice cover on the swarming behaviour of Antarctic krill, *Euphausia superba*. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 24–30.

Bright, T., Ferrari, F., Martin, D. & Franceschini, G. A. (1972). Effects of a total solar eclipse on the vertical distribution of certain oceanic zooplankters. *Limnology and Oceanography* **17**, 296–301.

Brink, K. (1983). The near-surface dynamics of coastal upwelling. *Progress in Oceanography* **12**, 223–257.

Brook, G. (1886). Report on the herring fishery of loch Fyne and the adjacent districts during 1885. *Fourth Annual Report of the Fishery Board for Scotland* **4**, 47–60.

Brook, G. & Calderwood, W. (1885). Report on the food of the herring. *Fourth Annual Report of the Fishery Board for Scotland* **3**, 102–128.

Brown, C. J. (1933). A limnological study of certain fresh-water Polyzoa with special reference to their statoblasts. *Transactions of the American Microscopical Society* **52**, 271–316.

Brun, P., Stamieszkin, K., Visser, A. W., Licandro, P., Payne, M. R. & Kiørboe, T. (2019). Climate change has altered zooplankton-fuelled carbon export in the North Atlantic. *Nature Ecology & Evolution* **3**, 416–423.

Bruno, M. C., Loftus, W. F., Reid, J. W. & Perry, S. A. (2001). Diapause in copepods (Crustacea) from ephemeral habitats with different hydroperiods in Everglades National Park (Florida, USA). *Hydrobiologia* **453**, 295–308.

Buchanan-Wollaston, H. (1911). On a new form of plankton-net designed to make truly vertical hauls in any weather. *ICES Journal of Marine Science* **1**, 9–14.

Buchanan, C. & Haney, J. F. (1980). Vertical migrations of zooplankton in the Arctic: a test of the environmental controls. In *Evolution and Ecology of Zooplankton Communities* (ed. W. C. Kerfoot), pp. 69–79. University Press of New England, Hanover.

Buskey, E. J. (1984). Swimming pattern as an indicator of the roles of copepod sensory systems in the recognition of food. *Marine Biology* **79**, 165–175.

Caceres, C. E. & Hairston, N. G. (1998). Benthic-pelagic coupling in planktonic crustaceans: the role of the benthos (with 4 figures). *Archiv Für Hydrobiologie Ergebnisse der Limnologie* **52**, 163–174.

Cáceres, C. E. & Tessier, A. J. (2004). To sink or swim: variable diapause strategies among *Daphnia* species. *Limnology and Oceanography* **49**, 1333–1340.

Calaban, M. J. & Makarewicz, J. (1982). The effect of temperature and density on the amplitude of vertical migration of *Daphnia magna*. *Limnology and Oceanography* **27**, 262–271.

Calderoni, A. & Tartari, G. A. (2001). Evolution of the water chemistry of Lake Orta after liming. *Journal of Limnology* **60**, 69–78.

Calman, W. (1909). Part 7 Appendiculata, third fascicle, Crustacea. In *A Treatise on Zoology* (ed. R. Lankester), pp. 1–333. Adam and Charles Black, London.

Campana, S. E., Dorey, A., Fowler, M., Joyce, W., Wang, Z., Wright, D. & Yashayaev, I. (2011). Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic. *PLoS One* **6**, e16854.

Campbell, R. G., Wagner, M. M., Teegarden, G. J., Boudreau, C. A. & Durbin, E. G. (2001). Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Marine Ecology Progress Series* **221**, 161–183.

Campbell, R. W. (2004). Reply to horizons article 'some ideas about the role of lipids in the life cycle of *Calanus finmarchicus*' Irigoien (2004): I. *Journal of Plankton Research* **26**, 979–980.

Campbell, R. W., Boutillier, P. & Dower, J. F. (2004). Ecophysiology of overwintering in the copepod *Neocalanus plumchrus*: changes in lipid and protein contents over a seasonal cycle. *Marine Ecology Progress Series* **280**, 211–226.

Carey, F. & Robinson, B. (1981). Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fisheries Bulletin* **79**, 277–292.

Carlisle, D. (1968). *Triops* (Entomostraca) eggs killed only by boiling. *Science* **161**, 279–280.

Carlisle, D. & Pitman, W. (1961). Diapause, neurosecretion and hormones in Copepoda. *Nature* **190**, 827–828.

Carlotti, F., Giske, J. & Werner, F. (2000). Modeling zooplankton dynamics. In *ICES Zooplankton Methodology Manual* (eds R. P. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal and M. Huntley), pp. 571–667. Academic Press, San Diego.

Carlotti, F. & Wolf, K. U. (1998). A Lagrangian ensemble model of *Calanus finmarchicus* coupled with a 1D ecosystem model. *Fisheries Oceanography* **7**, 191–204.

Carr, S. D., Capet, X. J., Mcwilliams, J. C., Pennington, J. T. & Chavez, F. P. (2008). The influence of diel vertical migration on zooplankton transport and recruitment in an upwelling region: estimates from a coupled behavioral-physical model. *Fisheries Oceanography* **17**, 1–15.

Cartamil, D. P. & Lowe, C. G. (2004). Diel movement patterns of ocean sunfish *Mola mola* off southern California. *Marine Ecology Progress Series* **266**, 245–253.

Cashmore, A., Jarillo, J. A., Wu, Y.-J. & Liu, D. (1999). Cryptochromes: blue light receptors for plants and animals. *Science* **284**, 760–765.

Chen, C. & Folt, C. (1996). Consequences of fall warming for zooplankton over wintering success. *Limnology and Oceanography* **41**, 1077–1086.

Cheng, C. (1947). On the fertility of marine Cladocera with a note on the formation of the resting egg in *Evadne nordmanni* Lovén and *Podon intermedius* Lilljeborg. *Journal of the Marine Biological Association of the United Kingdom* **26**, 551–561.

Chun, C. (1888). Die pelagische Tierwelt in größeren Meerestiefen und ihre Beziehungen zu der Oberflächenfauna. In *Bibliotheca Zoologica* (ed. R. Leukart), pp. 1–106. Cassel (verlag von Theodor Fischer), Munich.

Churnside, J. H. & Thorne, R. E. (2005). Comparison of airborne lidar measurements with 420 kHz echo-sounder measurements of zooplankton. *Applied Optics* **44**, 5504–5511.

Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y. & Irigoien, X. (2014). Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES Journal of Marine Science* **71**, 241–253.

Cisewski, B. & Strass, V. H. (2016). Acoustic insights into the zooplankton dynamics of the eastern Weddell Sea. *Progress in Oceanography* **144**, 62–92.

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**, 78–94.

Clark, K. A. J., Brierley, A. S. & Pond, D. W. (2012). Composition of wax esters is linked to diapause behavior of *Calanus finmarchicus* in a sea loch environment. *Limnology and Oceanography* **57**, 65–75.

Clarke, A. (1988). Seasonality in the Antarctic marine environment. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry* **90**, 461–473.

Clarke, E. (1942). A modification of the Juday plankton trap. *Special Publications of Limnological Society of America* **8**, 1–4.

Clarke, G. L. (1930). Change of phototropic and geotropic signs in *Daphnia* induced by changes of light intensity. *Journal of Experimental Biology* **7**, 109–131.

Clarke, G. L. (1934). Further observations on the diurnal migration of copepods in the gulf of Maine. *The Biological Bulletin* **67**, 432–455.

Coffey, D. M., Carlisle, A. B., Hazen, E. L. & Block, B. A. (2017). Oceanographic drivers of the vertical distribution of a highly migratory, endothermic shark. *Scientific Reports* **7**, 10434.

Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* **12**, 119–129.

Cohen, J. H., Berge, J., Moline, M. A., Sørensen, A. J., Last, K. S., Falk-Petersen, S., Renaud, P. E., Leu, E., Grenvald, J. C. & Cottier, F. R. (2015). Is ambient light during the high Arctic polar night sufficient to act as a visual cue for zooplankton? *PLoS One* **10**, e0126247.

Cohen, J. H. & Forward, R. B. (2002). Spectral sensitivity of vertically migrating marine copepods. *The Biological Bulletin* **203**, 307–314.

Cohen, J. H. & Forward, R. B. (2009). Zooplankton diel vertical migration—a review of proximate control. *Oceanography and Marine Biology: An Annual Review* **47**, 89–122.

Conover, R. J. (1965). Notes on the molting cycle, development of sexual characters and sex ratio in *Calanus hyperboreus*. *Crustaceana* **8**, 308–320.

Conover, R. J. (1988). Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. In *Biology of Copepods: Proceedings of the Third International Conference on Copepoda* (eds G. A. Boxshall and H. K. Schminke), pp. 127–142. Springer Netherlands, Dordrecht.

Conover, R. J. & Siferd, T. D. (1993). Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. *Arctic* **46**, 303–311.

Cooke, R., Bell, W., Ford, J. & Terhune, L. (1970). *An Opto-Electronic Plankton Sizer*. Fisheries Research Board of Canada, Technical Report no. 172, pp. 1–40. Fisheries Research Board of Canada, Nanaimo.

Cooke, S. L., Williamson, C. E., Leech, D. M., Boeing, W. J. & Torres, L. (2008). Effects of temperature and ultraviolet radiation on diel vertical migration of freshwater crustacean zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1144–1152.

Cooley, J. M. (1971). The effect of temperature on the development of resting eggs of *Diaptomus oregonensis* Lillj (Copepoda: Calanoida). *Limnology and Oceanography* **16**, 921–926.

Corkett, C. J. & McLaren, I. A. (1979). The biology of *Pseudocalanus*. In *Advances in Marine Biology* (eds F. S. Russell and M. Yonge), pp. 1–231. Academic Press, New York.

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**, 2586–2599.

Cotton, P. A. (2003). Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 12219–12222.

Cowen, R. K. & Guigand, C. M. (2008). In situ ichthyoplankton imaging system (ISIIS): system design and preliminary results. *Limnology and Oceanography: Methods* **6**, 126–132.

Coyle, K. O. & Pinchuk, A. I. (2005). Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

properties, species depth preferences and vertical migration behavior. *Deep Sea Research Part II: Topical Studies in Oceanography* **52**, 217–245.

Cresswell, K., William, H. & Sword, G. (2011). Understanding the evolution of migration through empirical examples. In *Animal Migration: A Synthesis* (eds E. Milner-Gulland, J. M. Mryxell and A. Sinclair), pp. 7–16. Oxford University Press, Oxford.

Criales-Hernández, M. I., Schwamborn, R., Graco, M., Ayón, P., Hirche, H. J. & Wolff, M. (2008). Zooplankton vertical distribution and migration off Central Peru in relation to the oxygen minimum layer. *Helgoland Marine Research* **62**, 85–100.

Cronin, T. W. & Forward, R. B. (1979). Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. *Science* **205**, 1020–1022.

Cushing, C. (1964). An apparatus for sampling drifting organisms in streams. *The Journal of Wildlife Management* **28**, 592–594.

Cushing, D. (1951). The vertical migration of planktonic crustacea. *Biological Reviews* **26**, 158–192.

Cuvier, G. (1817). *Le Règne Animal*. Chez Deterville, Paris.

D'Abramo, L. R. (1980). Ingestion rate decrease as the stimulus for sexuality in populations of *Moina macrocopa* 1. *Limnology and Oceanography* **25**, 422–429.

Daase, M., Falk-Petersen, S., Varpe, Ø., Darnis, G., Søreide, J. E., Wold, A., Leu, E., Berge, J., Philippe, B. & Fortier, L. (2013a). Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 871–884.

Daase, M., Hop, H. & Falk-Petersen, S. (2016). Small-scale diel vertical migration of zooplankton in the high Arctic. *Polar Biology* **39**, 1213–1223.

Daase, M., Varpe, Ø. & Falk-Petersen, S. (2013b). Non-consumptive mortality in copepods: occurrence of *Calanus* spp. carcasses in the Arctic Ocean during winter. *Journal of Plankton Research* **36**, 129–144.

Dagorn, L., Bach, P. & Josse, E. (2000). Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* **136**, 361–371.

Dahms, H.-U. (1995). Dormancy in the Copepoda—an overview. *Hydrobiologia* **306**, 199–211.

Dale, T., Bagøien, E., Melle, W. & Kaartvedt, S. (1999). Can predator avoidance explain varying overwintering depth of *Calanus* in different oceanic water masses? *Marine Ecology Progress Series* **179**, 113–121.

Danks, H. V. (1987). *Insect Dormancy: An Ecological Perspective*. Biological Survey of Canada (Terrestrial Artropods), Ottawa.

Darnis, G. & Fortier, L. (2014). Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen gulf (Beaufort Sea, Arctic Ocean). *Journal of Plankton Research* **36**, 1092–1108.

Darwin, C. (1833). *Charles Darwin's Diary of the Voyage of H.M.S. "Beagle"*. Macmillan Publishers, New York.

David, P. M. (1956). The distribution of *Sagitta gazellae* Ritter-Zahony. *Discovery Reports* **27**, 237–277.

David, P. M. (1958). The distribution of the Chaetognatha of the Southern Ocean. *Discovery Reports* **29**, 199–228.

Davies, T. W., Duffy, J. P., Bennie, J. & Gaston, K. J. (2014). The nature, extent, and ecological implications of marine light pollution. *Frontiers in Ecology and the Environment* **12**, 347–355.

Davis, C. S., Gallager, S. M. & Solow, A. R. (1992). Microaggregations of oceanic plankton observed by towed video microscopy. *Science* **257**, 230–232.

Davis, C. S., Thwaites, F. T., Gallager, S. M. & Hu, Q. (2005). A three-axis fast-tow digital video plankton recorder for rapid surveys of plankton taxa and hydrography. *Limnology and Oceanography: Methods* **3**, 59–74.

Dawidowicz, P. & Loose, C. J. (1992a). Cost of swimming by *Daphnia* during diel vertical migration. *Limnology and Oceanography* **37**, 665–669.

Dawidowicz, P. & Loose, C. J. (1992b). Metabolic costs during predator-induced dielvertical migration of *Daphnia*. *Limnology and Oceanography* **37**, 1589–1595.

Dawidowicz, P. & Pijanowska, J. (2018). Diel vertical migration of aquatic crustaceans—adaptive role, underlying mechanisms, and ecosystem consequences. In *The Natural History of the Crustacea: Life Histories* (eds M. Thiel and G. Welborn), pp. 231–256. Oxford University Press, New York.

Dawson, J. K. (1978). Vertical distribution of *Calanus hyperboreus* in the Central Arctic Ocean 1. *Limnology and Oceanography* **23**, 950–957.

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

de Robertis, A., Jaffe, J. S. & Ohman, M. D. (2000). Size-dependent visual predation risk and the timing of vertical migration in zooplankton. *Limnology and Oceanography* **45**, 1838–1844.

de Roeck, E. R., Artois, T. & Brendonck, L. (2005). Consumptive and non-consumptive effects of turbellarian (*Mesostoma* sp.) predation on anostracans. *Hydrobiologia* **542**, 103–111.

de Senerpont Domis, L. N., Mooij, W. M., Hülsmann, S., van Nes, E. H. & Scheffer, M. (2007). Can overwintering versus diapausing strategy in *Daphnia* determine match–mismatch events in zooplankton–algae interactions? *Oecologia* **150**, 682–698.

de Stasio, B. T. Jr., Hill, D. K., Kleinhans, J. M., Nibbelink, N. P. & Magnuson, J. J. (1996). Potential effects of global climate change on small north-temperate lakes: physics, fish, and plankton. *Limnology and Oceanography* **41**, 1136–1149.

Decaestecker, E., de Meester, L. & Ebert, D. (2002). In deep trouble: habitat selection constrained by multiple enemies in zooplankton. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 5481–5485.

Demarcq, H. (2009). Trends in primary production, sea surface temperature and wind in upwelling systems (1998–2007). *Progress in Oceanography* **83**, 376–385.

Dewar, W. K., Bingham, R. J., Iverson, R., Nowacek, D. P., St Laurent, L. C. & Wiebe, P. H. (2006). Does the marine biosphere mix the ocean? *Journal of Marine Research* **64**, 541–561.

Dickson, R. R. (1972). On the relationship between ocean transparency and the depth of sonic scattering layers in the North Atlantic. *ICES Journal of Marine Science* **34**, 416–422.

Dingle, H. & Drake, V. A. (2007). What is migration? *Bioscience* **57**, 113–121.

Dini, M. L. & Carpenter, S. R. (1992). Fish predators, food availability and diel vertical migration in *Daphnia*. *Journal of Plankton Research* **14**, 359–377.

Dodson, S. I. (1990). Predicting diel vertical migration of zooplankton. *Limnology and Oceanography* **35**, 1195–1200.

Dodson, S. I., Tollrian, R. & Lampert, W. (1997). *Daphnia* swimming behavior during vertical migration. *Journal of Plankton Research* **19**, 969–978.

Doubek, J. P., Campbell, K. L., Doubek, K. M., Hamre, K. D., Lofton, M. E., McClure, R. P., Ward, N. K. & Carey, C. C. (2018). The effects of hypolimnetic anoxia on the diel vertical migration of freshwater crustacean zooplankton. *Ecosphere* **9**, e02332.

Douglass, J. K., Wilson, J. H. & Forward, R. B. (1992). A tidal rhythm in phototaxis of larval grass shrimp (*Palaemonetes pugio*). *Marine Behaviour and Physiology* **19**, 159–173.

Drillet, G., Hansen, B. W. & Kiørboe, T. (2011). Resting egg production induced by food limitation in the calanoid copepod *Acartia tonsa*. *Limnology and Oceanography* **56**, 2064–2070.

Ducklow, H. W., Steinberg, D. K. & Buesseler, K. O. (2001). Upper Ocean carbon export and the biological pump. *Oceanography* **14**, 50–58.

Duffy, M. A., Housley, J. M., Penczykowski, R. M., Cáceres, C. E. & Hall, S. R. (2011). Unhealthy herds: indirect effects of predators enhance two drivers of disease spread. *Functional Ecology* **25**, 945–953.

Dunn, J., Hall, C., Heath, M. R., Mitchell, R. & Ritchie, B. (1993a). ARIES—a system for concurrent physical, biological and chemical sampling at sea. *Deep Sea Research Part I: Oceanographic Research Papers* **40**, 867–878.

Dunn, J., Mitchell, R., Urquhart, G. & Ritchie, B. (1993b). LOCHNESS—a new multi-net midwater sampler. *ICES Journal of Marine Science* **50**, 203–212.

Dupont, N. & Aksnes, D. L. (2011). Effects of bottom depth and water clarity on the vertical distribution of *Calanus* spp. *Journal of Plankton Research* **34**, 263–266.

Dupont, N., Klevjer, T., Kaartvedt, S. & Aksnes, D. L. (2009). Diel vertical migration of the deep-water jellyfish *Periphylla periphylla* simulated as individual responses to absolute light intensity. *Limnology and Oceanography* **54**, 1765–1775.

Durbin, E. G., Runge, J. A., Campbell, R., Garrahan, P., Casas, M. & Plourde, S. (1997). Late fall-early winter recruitment of *Calanus finmarchicus* on Georges Bank. *Marine Ecology Progress Series* **151**, 103–114.

Džeroski, S. (2001). Applications of symbolic machine learning to ecological modelling. *Ecological Modelling* **146**, 263–273.

Economou, G., Christou, E., Giannakourou, A., Gerasopoulos, E., Georgopoulos, D., Kotoulas, V., Lyra, D., Tsakalis, N., Tzortziou, M. & Vahamidis, P. (2008). Eclipse effects on field crops and marine zooplankton: the 29 march 2006 total solar eclipse. *Atmospheric Chemistry and Physics* **8**, 4665–4676.

Edgerton, H. E. & Hoadley, L. D. (1955). Cameras and lights for underwater use. *SMPTE Journal* **64**, 345–350.

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W. & Silk, J. R. D. (2010). Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 2078–2081.

Ehrenberg, J. (1974). Two applications for a dual-beam transducer in hydroacoustic fish assessment systems. In *Ocean '74 - IEEE International Conference on Engineering in the Ocean Environment*, pp. 152–155. IEEE, New York.

Eiane, K. & Parisi, D. (2001). Towards a robust concept for modelling zooplankton migration. *Sarsia* **86**, 465–475.

Ekvall, M. T., Bianco, G., Linse, S., Linke, H., Bäckman, J. & Hansson, L.-A. (2013). Three-dimensional tracking of small aquatic organisms using fluorescent nanoparticles. *PLoS One* **8**, e78498.

Elgmork, K. (1955). A resting stage without Encystment in the animal cycle of the freshwater copepod *Cyclops strenuus strenuus*. *Ecology* **36**, 739–743.

Elgmork, K. (1959). Seasonal occurrence of *Cyclops strenuus strenuus* in relation to environment in small water bodies in southern Norway. *Folia Limnologica Scandinavica* **11**, 1–196.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Elgmork, K. (1962). A bottom resting stage in the planktonic freshwater copepod *Cyclops scutifer* Sars. *Oikos* **13**, 306–310.

Elgmork, K. (1967). Ecological aspects of diapause in copepods. In *Proceedings of Symposium on Crustacea*, pp. 947–954. Marine Biological Association of India, Cochin.

Elgmork, K., Halvorsen, G., Eie, J. A. & Langeland, A. (1990). Coexistence with similar life cycles in two species of freshwater copepods (Crustacea). *Hydrobiologia* **208**, 187–199.

Engel, M. & Hirche, H.-J. (2004). Seasonal variability and inter-specific differences in hatching of calanoid copepod resting eggs from sediments of the German bight (North Sea). *Journal of Plankton Research* **26**, 1083–1093.

Enright, J. T. (1977). Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. *Limnology and Oceanography* **22**, 856–872.

Esterly, C. O. (1917). The occurrence of a rhythm in the geotropism of two species of plankton copepods when certain recurring external conditions are absent. *University of California Publications of Zoology* **8**, 1–7.

Esterly, C. O. (1919). Reactions of various plankton animals with reference to their diurnal migrations. *University of California Publications of Zoology* **19**, 1–83.

Everett, J. D., Baird, M. E., Buchanan, P., Bulman, C., Davies, C., Downie, R., Griffiths, C., Heneghan, R., Kloser, R. J., Laiolo, L., Lara-Lopez, A., Lozano-Montes, H., Matear, R. J., McEnnulty, F., Robson, B., et al. (2017). Modeling what we sample and sampling what we model: challenges for zooplankton model assessment. *Frontiers in Marine Science* **4**, 77.

Ewald, W. F. (1910). Über Orientierung, Lokomotion und Lichtreaktionen einiger Cladoceren und deren Bedeutung für die Theorie der Tropismen. *Biologisches Centralblatt* **30**, 1–16.

Ewald, W. F. (1912). On artificial modification of light reactions and the influence of electrolytes on phototaxis. *Journal of Experimental Zoology* **13**, 591–612.

Eyden, D. (1923). Specific gravity as a factor in the vertical distribution of plankton. *Biological Reviews* **1**, 49–55.

Eyring, C. F., Christensen, R. J. & Raitt, R. W. (1948). Reverberation in the sea. *The Journal of the Acoustical Society of America* **20**, 462–475.

Eysteinsson, S. T., Gudjónsdóttir, M., Jónasdóttir, S. H. & Arason, S. (2018). Review of the composition and current utilization of *Calanus finmarchicus* – possibilities for human consumption. *Trends in Food Science & Technology* **79**, 10–18.

Falk-Petersen, S., Mayzaud, P., Kattner, G. & Sargent, J. R. (2009). Lipids and life strategy of Arctic *Calanus*. *Marine Biology Research* **5**, 18–39.

Falk-Petersen, S., Pavlov, V., Timofeev, S. & Sargent, J. R. (2007). Climate variability and possible effects on arctic food chains: the role of *Calanus*. In *Arctic Alpine Ecosystems and People in a Changing Environment* (eds J. Ørbaek, R. Kallenborn, I. Tombre, E. N. Hegseth, S. Falk-Petersen and A. Hoel), pp. 147–166. Springer, Heidelberg.

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**, 105–119.

Fels, D., Lee, V. A. & Ebert, D. (2004). The impact of microparasites on the vertical distribution of *Daphnia magna*. *Archiv für Hydrobiologie* **161**, 65–80.

Fernández, C. E., Campero, M., Bianco, G., Ekvall, M. T., Rejas, D., Uvo, C. B. & Hansson, L.-A. (2020). Local adaptation to UV radiation in zooplankton: a behavioral and physiological approach. *Ecosphere* **11**, e03081.

Fernö, A., Pitcher, T. J., Melle, W., Nøttestad, L., Mackinson, S., Hollingworth, C. & Misund, O. A. (1998). The challenge of the herring in the Norwegian sea: making optimal collective spatial decisions. *Sarsia* **83**, 149–167.

Field-dodgson, M. S. (1985). A simple and efficient drift sampler. *New Zealand Journal of Marine and Freshwater Research* **19**, 167–172.

Fiksen, Ø. (1997). Allocation patterns and diel vertical migration: modeling the optimal *Daphnia*. *Ecology* **78**, 1446–1456.

Fiksen, Ø. (2000). The adaptive timing of diapause–a search for evolutionarily robust strategies in *Calanus finmarchicus*. *ICES Journal of Marine Science* **57**, 1825–1833.

Fiksen, Ø. & Carlotti, F. (1998). A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. *Sarsia* **83**, 129–147.

Fiksen, Ø. & Giske, J. (1995). Vertical distribution and population dynamics of copepods by dynamic optimization. *ICES Journal of Marine Science* **52**, 483–503.

Fiksen, Ø., Varpe, Ø. & Kaartvedt, S. (2004). Reply to horizons article 'some ideas about the role of lipids in the life cycle of *Calanus finmarchicus*' Irigoien (2004): II. *Journal of Plankton Research* **26**, 980–981.

Finlay, K., Beisner, B. E. & Barnett, A. J. (2007). The use of the laser optical plankton counter to measure zooplankton size, abundance, and biomass in small freshwater lakes. *Limnology and Oceanography: Methods* **5**, 41–49.

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**, 1547–1557.

Fischer, J. M., Nicolai, J. L., Williamson, C. E., Persaud, A. D. & Lockwood, R. S. (2006). Effects of ultraviolet radiation on diel vertical migration of crustacean zooplankton: an in situ mesocosm experiment. *Hydrobiologia* **563**, 217–224.

Fischer, J. M., Olson, M. H., Theodore, N., Williamson, C. E., Rose, K. C. & Hwang, J. (2015). Diel vertical migration of copepods in mountain lakes: the changing role of ultraviolet radiation across a transparency gradient. *Limnology and Oceanography* **60**, 252–262.

Forbes, S. (1882). On some Entomostraca of Lake Michigan and adjacent waters. *The American Naturalist* **16**, 537–542.

Forel, F. (1878). Faunistische studien in den süsswasserseen der Schweiz. In *Zeitschrift Wissenschaftliche Zooloogie* (eds C. T. V. Siebold, A. V. Kölliker and E. Ehlers), pp. 383–391. Verlag von Wilhelm Engelmann, Leipzig.

Forel, F. (1882). XXXII.—The pelagic fauna of freshwater lakes. *Journal of Natural History* **10**, 320–325.

Forster, J. & Hirst, A. G. (2012). The temperature-size rule emerges from ontogenetic differences between growth and development rates. *Functional Ecology* **26**, 483–492.

Fortier, L. & Harris, R. P. (1989). Optimal foraging and density-dependent competition in marine fish larvae. *Marine Ecology Progress Series* **51**, 19–33.

Fortier, M., Fortier, L., Hattori, H., Saito, H. & Legendre, L. (2001). Visual predators and the diel vertical migration of copepods under Arctic Sea ice during the midnight sun. *Journal of Plankton Research* **23**, 1263–1278.

Forward, R. B. (1976). Light and diurnal vertical migration: Photobehavior and Photophysiology of plankton. In *Photochemical and Photobiological Reviews* (ed. K. C. Smith), pp. 157–209. Springer US, Boston.

Forward, R. B. (1988). Diel vertical migration: zooplankton photobiology and behaviour. *Oceanography and Marine Biology - An Annual Review* **26**, 1–393.

Foulds, J. & Roff, J. (1976). Oxygen consumption during simulated vertical migration in *Mysis relicta* (Crustacea, Mysidacea). *Canadian Journal of Zoology* **54**, 377–385.

Fraser, J. (1968). Standardization of zooplankton sampling methods at sea. In *Zooplankton Sampling, Part II* (ed. J. Tranter), pp. 149–168. UNESCO press, Paris.

Freitag, L., Ball, K., Partan, J., Koski, P. & Singh, S. (2015). Long range acoustic communications and navigation in the Arctic. In *Proceedings of the Oceans'15 MTS/IEEE Washington Conference, October 19–22, 2015*, pp. 1–5. IEEE, New York.

Frič, A. & Vávra, V. (1897). Untersuchung zweier Böhmerwaldseen, des Schwarzen und des Teufelssees. *Archiv der Naturwissenschaftlichen Landesdurchforschung von Böhmen* **10**, 1–74.

Frisch, D., Green, A. J. & Figuerola, J. (2007). High dispersal capacity of a broad spectrum of aquatic invertebrates via waterbirds. *Aquatic Sciences* **69**, 568–574.

Frost, B. W. & Bollens, S. M. (1992). Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1137–1141.

Fryer, G. (1996). Diapause, a potent force in the evolution of freshwater crustaceans. *Hydrobiologia* **320**, 1–14.

Fryer, G. (1997). The horse-trough ostracod *Heterocypris incongruens*. *Natura* **122**, 121–135.

Fryer, G. & Smyly, W. J. P. (1954). X.—Some remarks on the resting stages of some freshwater Cyclopoid and Harpacticoid copepods. *Annals and Magazine of Natural History* **7**, 65–72.

Fuchs, T. H. (1882). Über die Pelagische Flora und Fauna. *Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* **7**, 49–70.

Gaardsted, F., Tande, K. S. & Basedow, S. L. (2010). Measuring copepod abundance in deep-water winter habitats in the NE Norwegian Sea: Intercomparison of results from laser optical plankton counter and multinet. *Fisheries Oceanography* **19**, 480–492.

Gabriel, W. & Thomas, B. (1988). Vertical migration of zooplankton as an evolutionarily stable strategy. *The American Naturalist* **132**, 199–216.

Garcia-Roger, E. M., Carmona, M. J. & Serra, M. (2006). Hatching and viability of rotifer diapausing eggs collected from pond sediments. *Freshwater Biology* **51**, 1351–1358.

Gaten, E., Tarling, G. A., Dowse, H., Kyriacou, C. & Rosato, E. (2008). Is vertical migration in Antarctic krill (*Euphausia superba*) influenced by an underlying circadian rhythm? *Journal of Genetics* **87**, 473–483.

Gehring, W. & Rosbash, M. (2003). The coevolution of blue-light photoreception and circadian rhythms. *Journal of Molecular Evolution* **57**, S286–S289.

Geoffroy, M., Robert, D., Darnis, G. & Fortier, L. (2011). The aggregation of polar cod (*Boreogadus saida*) in the deep Atlantic layer of ice-covered Amundsen gulf (Beaufort Sea) in winter. *Polar Biology* **34**, 1959–1971.

George, D. (1973). Diapause in *Cyclops vicinus*. *Oikos* **24**, 136–142.

Gerritsen, J. (1982). Behavioral response of *Daphnia* to rate of temperature change: possible enhancement of vertical migration. *Limnology and Oceanography* **27**, 254–261.

Gibbons, M. J. & Stuart, V. (1994). Feeding and vertical migration of the chaetognath *Sagitta friderici* (Ritter-Zahony, 1911) in the southern Benguela during spring 1987, with notes on seasonal variability of feeding ecology. *South African Journal of Marine Science* **14**, 361–372.

Gilbert, J. J. (1963). Mictic female production in the rotifer *Brachionus calyciflorus*. *Journal of Experimental Zoology* **153**, 113–123.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Gilbert, J. J. & Hampton, S. E. (2001). Diel vertical migrations of zooplankton in a shallow, fishless pond: a possible avoidance-response cascade induced by notonectids. *Freshwater Biology* **46**, 611–621.

Giraudet, P. & Glotin, H. (2006). Real-time 3D tracking of whales by echo-robust precise TDOA estimates with a widely-spaced hydrophone array. *Applied Acoustics* **67**, 1106–1117.

Giske, J., Rosland, R., Berntsen, J. & Fiksen, Ø. (1997). Ideal free distribution of copepods under predation risk. *Ecological Modelling* **95**, 45–59.

Gislason, A. (2003). Life-cycle strategies and seasonal migrations of oceanic copepods in the Irminger Sea. In *Migrations and Dispersal of Marine Organisms* (eds M. B. Jones, A. Ingólfsson, E. Ólafsson, G. V. Helgason, K. Gunnarsson and J. Svavarsson), pp. 195–209. Springer, Dordrecht.

Gislason, A. (2018). Life cycles and seasonal vertical distributions of copepods in the Iceland Sea. *Polar Biology* **41**, 2575–2589.

Gislason, A. & Astthorsson, O. S. (2002). The food of Norwegian spring-spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton. *Sarsia: North Atlantic Marine Science* **87**, 236–247.

Gislason, A., Eiane, K. & Reynisson, P. (2007). Vertical distribution and mortality of *Calanus finmarchicus* during overwintering in oceanic waters southwest of Iceland. *Marine Biology* **150**, 1253–1263.

Giuliano, G., Hoffman, N., Ko, K., Scolnik, P. & Cashmore, A. (1988). A light-entrained circadian clock controls transcription of several plant genes. *The EMBO Journal* **7**, 3635–3642.

Glaholt, S. P., Kennedy, M. L., Turner, E., Colbourne, J. K. & Shaw, J. R. (2016). Thermal variation and factors influencing vertical migration behavior in *Daphnia* populations. *Journal of Thermal Biology* **60**, 70–78.

Gleiss, A. C., Wright, S., Liebsch, N., Wilson, R. P. & Norman, B. (2013). Contrasting diel patterns in vertical movement and locomotor activity of whale sharks at Ningaloo reef. *Marine Biology* **160**, 2981–2992.

Gliwicz, Z. M. (1986a). A lunar cycle in zooplankton. *Ecology* **67**, 883–897.

Gliwicz, Z. M. (1986b). Predation and the evolution of vertical migration in zooplankton. *Nature* **320**, 746–748.

Gliwicz, Z. M. & Pijanowska, J. (1988). Effect of predation and resource depth distribution on vertical migration of zooplankton. *Bulletin of Marine Science* **43**, 695–709.

Gorbunova, N., Evseenko, S. & Garetovsky, S. (1985). Distribution of ichthyoplankton in the frontal zones of the Peruvian waters. *Journal of Ichthyology* **25**, 67–79.

Gorsky, G., Aldorf, C., Kage, M., Picheral, M. & Garcia, Y. (1992). Vertical distribution of suspended aggregates determined by a new underwater video profiler. *Annales de l'Institut Océanographique* **68**, 275–280.

Gran, H. H. (1902). Das Plankton des Norwegischen Nordmeeres von biologischen und hydrografischen Gesichtpunkten behandelt. *Report on Norwegian Fishery and Marine Investigations* **2**, 1–219.

Green, W. R. (1919). Studies in the life cycle of *Simocephalus vetulus*. *The Biological Bulletin* **37**, 49–95.

Greene, C. H. (1986). Patterns of prey selection: implications of predator foraging tactics. *The American Naturalist* **128**, 824–839.

Greene, C. H., Wiebe, P. H. & Burczynski, J. (1989). Analyzing zooplankton size distributions using high-frequency sound. *Limnology and Oceanography* **34**, 129–139.

Greenlaw, C., Player, R. & Samilo, U. (1994). Applications of multifrequency acoustics: spatial patterns in a freshwater lake. *The Journal of the Acoustical Society of America* **96**, 3298–3298.

Grice, G. & Marcus, N. H. (1981). Dormant eggs of marine copepods. *Oceanography and Marine Biology - An Annual Review* **19**, 125–140.

Grigg, H. & Bardwell, S. J. (1982). Seasonal observations on moulting and maturation in stage V copepodites of *Calanus finmarchicus* from the firth of Clyde. *Journal of the Marine Biological Association of the United Kingdom* **62**, 315–327.

Grigor, J. J., Søreide, J. E. & Varpe, Ø. (2014). Seasonal ecology and life-history strategy of the high-latitude predatory zooplankter *Parasagitta elegans*. *Marine Ecology Progress Series* **499**, 77–88.

Grindley, J. R. (1964). Effect of low-salinity water on the vertical migration of estuarine plankton. *Nature* **203**, 781–782.

Grosbois, G., Mariash, H. L., Schneider, T. & Rautio, M. (2017). Under-ice availability of phytoplankton lipids is key to freshwater zooplankton winter survival. *Scientific Reports* **7**, 11543.

Grossart, H.-P., Dziallas, C., Leunert, F. & Tang, K. W. (2010). Bacteria dispersal by hitchhiking on zooplankton. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 11959–11964.

Grosvenor, G. & Smith, G. (1913). Memoirs: the life-cycle of *Monia rectirostris*. *Journal of Cell Science* **2**, 511–522.

Guo, B., Yu, J., Yuan, G., Liu, H., Xu, W., Hou, R. & Guo, G. (2018). Miniaturized digital inline holographic camera for in-situ plankton detection. In *Proceedings of the SPIE/COS PHOTONICS ASIA, 11–13 October, 2018, Advanced Sensor Systems and Applications VIII*, 108210R. SPIE, Beijing.

Gyllström, M. (2004). Induction and termination of diapause in a freshwater zooplankton community. *Archiv für Hydrobiologie* **161**, 81–97.

Gyllström, M. & Hansson, L.-A. (2004). Dormancy in freshwater zooplankton: induction, termination and the importance of benthic-pelagic coupling. *Aquatic Sciences* **66**, 274–295.

Häfker, N. S., Meyer, B., Last, K. S., Pond, D. W., Hüppe, L. & Teschke, M. (2017). Circadian clock involvement in zooplankton Diel vertical migration. *Current Biology* **27**, 2194–2201.

Häfker, N. S., Teschke, M., Last, K. S., Pond, D. W., Hüppe, L. & Meyer, B. (2018). *Calanus finmarchicus* seasonal cycle and diapause in relation to gene expression, physiology, and endogenous clocks. *Limnology and Oceanography* **63**, 2815–2838.

Hagen, W. & Auel, H. (2001). Seasonal adaptations and the role of lipids in oceanic zooplankton. *Zoology* **104**, 313–326.

Hain, M. P., Sigman, D. M. & Haug, G. H. (2014). 8.18 - The biological pump in the past. In *Treatise on Geochemistry* (eds H. D. Holland and K. K. Turekian), pp. 485–517. Elsevier, Oxford.

Hairston, N. G. & Dillon, T. A. (1990). Fluctuating selection and response in a population of freshwater copepods. *Evolution* **44**, 1796–1805.

Hairston, N. G. & Fox, J. A. (2009). Egg banks. In *Encyclopedia of Inland Waters* (ed. G. E. Likens), pp. 659–666. Academic Press, Oxford.

Hairston, N. G. & Olds, E. J. (1986). Partial photoperiodic control of diapause in three populations of the freshwater copepod *Diaptomus sanguineus*. *The Biological Bulletin* **171**, 135–142.

Hairston, N. G., Olds, E. J. & Munns, W. R. Jr. (1985). Bet-hedging and environmentally cued diapause strategies of diaptomid copepods: with 3 figures in the text. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen* **22**, 3170–3177.

Hairston, N. G. & Walton, W. E. (1986). Rapid evolution of a life history trait. *Proceedings of the National Academy of Sciences of the United States of America* **83**, 4831–4833.

Hairston, N. G., Walton, W. E. & Li, K. T. (1983). The causes and consequences of sex-specific mortality in a freshwater copepod 1. *Limnology and Oceanography* **28**, 935–947.

Hall, D. J. (1964). An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. *Ecology* **45**, 94–112.

Halvorsen, E., Tande, K. S., Edvardsen, A., Slagstad, D. & Pedersen, O. P. (2003). Habitat selection of overwintering *Calanus finmarchicus* in the NE Norwegian Sea and shelf waters off northern Norway in 2000–02. *Fisheries Oceanography* **12**, 339–351.

Hand, S. C. (1991). Metabolic dormancy in aquatic invertebrates. In *Advances in Comparative and Environmental Physiology* (eds M. A. Castellini, B. Fiévet, S. C. Hand, R. Motais, B. Pelster and R. E. Weber), pp. 1–50. Springer, Berlin.

Haney, J. F. (1993). Environmental control of diel vertical migration behaviour. *Archiv Für Hydrobiologie Ergebnisse der Limnologie* **39**, 1–17.

Haney, J. F. & Hall, D. J. (1975). Diel vertical migration and filter-feeding activities of *Daphnia*. *Archiv für Hydrobiologie* **75**, 413–441.

Hansen, A.-M. & Hairston, N. G. (1998). Food limitation in a wild cyclopoid copepod population: direct and indirect life history responses. *Oecologia* **115**, 320–330.

Hansson, S., Fagerberg, T. & Gorokhova, E. (2004). Predation by herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) on *Cercopagis pengoi* in a western Baltic Sea bay. *ICES Journal of Marine Science* **61**, 959–965.

Hardy, A. C. (1935). The continuous plankton recorder: a new method of survey. *Rapports et Proces-Verbaux des Reunions. Conseil International pour l'Exploration de la Mer* **95**, 36–47.

Hardy, A. C. (1936). Plankton ecology and the hypothesis of animal exclusion. *Proceedings of the Linnean Society of London* **148**, 64–70.

Hardy, A. C. & Gunther, E. R. (1935). The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. *Discovery Reports* **11**, 1–456.

Hardy, L. M. & Raymond, L. R. (1980). The breeding migration of the mole salamander, *Ambystoma talpoideum*, in Louisiana. *Journal of Herpetology* **14**, 327–335.

Harris, J. E. (1963). The role of endogenous rhythms in vertical migration. *Journal of the Marine Biological Association of the United Kingdom* **43**, 153–166.

Haupt, F., Stockenreiter, M., Baumgartner, M., Boersma, M. & Stibor, H. (2009). *Daphnia* diel vertical migration: implications beyond zooplankton. *Journal of Plankton Research* **31**, 515–524.

Hawkes, L. A., Balachandran, S., Batbayar, N., Butler, P. J., Frappell, P. B., Milsom, W. K., Tseveenmyadag, N., Newman, S. H., Scott, G. R. & Sathiyaselvam, P. (2011). The trans-Himalayan flights of bar-headed geese (*Anser indicus*). *Proceedings of the National Academy of Sciences of the United States of America* **108**, 9516–9519.

Hays, G. C. (1995). Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*. *Limnology and Oceanography* **40**, 1461–1465.

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* **503**, 163–170.

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**, 2050–2054.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hays, G. C., Proctor, C., John, A. & 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**, 1621–1629.

Hays, G. C., Warner, A. J. & Lefevre, D. (1996). Long-term changes in the diel vertical migration behaviour of zooplankton. *Marine Ecology Progress Series* **141**, 149–159.

Head, E. J. H. & Harris, L. R. (1985). Physiological and biochemical changes in *Calanus hyperboreus* from Jones sound NWT during the transition from summer feeding to overwintering condition. *Polar Biology* **4**, 99–106.

Heard, M., Rogers, P. J., Bruce, B. D., Humphries, N. E. & Huveneers, C. (2018). Plasticity in the diel vertical movement of two pelagic predators (*Prionace glauca* and *Alopias vulpinus*) in the southeastern Indian Ocean. *Fisheries Oceanography* **27**, 199–211.

Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J. G., Gallego, A. & Hainbucher, D. (1999). Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fisheries Oceanography* **8**, 163–176.

Heath, M. R., Boyle, P. R., Gislason, A., Gurney, W. S. C., Hay, S. J., Head, E. J. H., Holmes, S., Ingvarsdóttir, A., Jónasdóttir, S. H., Lindeque, P., Pollard, R. T., Rasmussen, J., Richards, K., Richardson, K., Smerdon, G. & Speirs, D. (2004). Comparative ecology of over-wintering *Calanus finmarchicus* in the northern North Atlantic, and implications for life-cycle patterns. *ICES Journal of Marine Science* **61**, 698–708.

Heath, M. R. & Jónasdóttir, S. H. (1999). Distribution and abundance of overwintering *Calanus finmarchicus* in the Faroe–Shetland Channel. *Fisheries Oceanography* **8**, 40–60.

Hebblewhite, M. & Merrill, E. H. (2007). Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* **152**, 377–387.

Hembre, L. K. & Megard, R. O. (2003). Seasonal and diel patchiness of a *Daphnia* population: an acoustic analysis. *Limnology and Oceanography* **48**, 2221–2233.

Henriksen, M. V., Jung-Madsen, S., Nielsen, T. G., Møller, E. F., Henriksen, K. V., Markager, S. & Hansen, B. W. (2012). Effects of temperature and food availability on feeding and egg production of *Calanus hyperboreus* from Disko Bay, western Greenland. *Marine Ecology Progress Series* **447**, 109–126.

Herdman, W. (1907). Plankton fishing off the Isle of Man. *Science* **26**, 551–554.

Herman, A. W. (1983). Vertical distribution patterns of copepods, chlorophyll, and production in northeastern Baffin Bay. *Limnology and Oceanography* **28**, 709–719.

Herman, A. W. (1988). Simultaneous measurement of zooplankton and light attenuance with a new optical plankton counter. *Continental Shelf Research* **8**, 205–221.

Herman, A. W. (1992). Design and calibration of a new optical plankton counter capable of sizing small zooplankton. *Deep Sea Research Part A. Oceanographic Research Papers* **39**, 395–415.

Herman, A. W., Beanlands, B. & Phillips, E. (2004). The next generation of optical plankton counter: the laser-OPC. *Journal of Plankton Research* **26**, 1135–1145.

Heron, A. (1982). A vertical free fall plankton net with no mouth obstructions. *Limnology and Oceanography* **27**, 380–383.

Heuch, P. A., Parsons, A. & Boxaspen, K. (1995). Diel vertical migration: a possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 681–689.

Hidalgo, P., Escribano, R. & Morales, C. E. (2005). Ontogenetic vertical distribution and diel migration of the copepod *Eucalanus inermis* in the oxygen minimum zone off northern Chile (20–21° S). *Journal of Plankton Research* **27**, 519–529.

Hill, A. (1991). A mechanism for horizontal zooplankton transport by vertical migration in tidal currents. *Marine Biology* **111**, 485–492.

Hind, A., Gurney, W. S. C., Heath, M. R. & Bryant, A. (2000). Overwintering strategies in *Calanus finmarchicus*. *Marine Ecology Progress Series* **193**, 95–107.

Hirche, H.-J. (1991). Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. *Polar Biology* **11**, 351–362.

Hirche, H.-J. (1996a). Diapause in the marine copepod, *Calanus finmarchicus*—a review. *Ophelia* **44**, 129–143.

Hirche, H.-J. (1996b). The reproductive biology of the marine copepod, *Calanus finmarchicus*—a review. *Ophelia* **44**, 111–128.

Hirche, H.-J., Hagen, W., Mumm, N. & Richter, C. (1994). The northeast water polynya, Greenland Sea. *Polar Biology* **14**, 491–503.

Hirche, H.-J., Muyakshin, S., Klages, M. & Auel, H. (2006). Aggregation of the Arctic copepod *Calanus hyperboreus* over the ocean floor of the Greenland Sea. *Deep Sea Research Part I: Oceanographic Research Papers* **53**, 310–320.

Hirche, H.-J. & Niehoff, B. (1996). Reproduction of the Arctic copepod *Calanus hyperboreus* in the Greenland Sea-field and laboratory observations. *Polar Biology* **16**, 209–219.

Hobaek, A. & Larsson, P. (1990). Sex determination in *Daphnia magna*. *Ecology* **71**, 2255–2268.

Hobbs, L., Banas, N. S., Cottier, F. R., Berge, J. & Daase, M. (2020). Eat or sleep: availability of winter prey explains mid-winter and spring activity in an Arctic *Calanus* population. *Frontiers in Marine Science* **7**, 541564.

Horning, M. & Trillmich, F. (1999). Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galapagos fur seals. *Proceedings of the Royal Society of London B: Biological Sciences* **266**, 1127–1132.

Hostetler, C. A., Behrenfeld, M. J., Hu, Y., Hair, J. W. & Schulien, J. A. (2018). Spaceborne Lidar in the study of marine systems. *Annual Review of Marine Science* **10**, 121–147.

Houston, A. I., McNamara, J. M. & Hutchinson, J. M. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **341**, 375–397.

Hoyle, W. (1889). On a deep sea tow-net for opening and shutting under water. *Proceedings and Transactions of the Liverpool Biological Society* **3**, 100–112.

Hozumi, A., Kaartvedt, S., Røstad, A., Berumen, M. L., Cochran, J. E. M. & Jones, B. H. (2018). Acoustic backscatter at a Red Sea whale shark aggregation site. *Regional Studies in Marine Science* **20**, 23–33.

Hugie, D. M. & Dill, L. M. (1994). Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology* **45**, 151–169.

Huntley, M. & Brooks, E. (1982). Effects of age and food availability on diel vertical migration of *Calanus pacificus*. *Marine Biology* **71**, 23–31.

Hüppe, L., Payton, L., Last, K., Wilcockson, D., Ershova, E. & Meyer, B. (2020). Evidence for oscillating circadian clock genes in the copepod *Calanus finmarchicus* during the summer solstice in the high Arctic. *Biology Letters* **16**, 20200257.

Huse, G., Melle, W., Skogen, M. D., Hjøllo, S. S., Svendsen, E. & Budgell, W. P. (2018). Modeling emergent life histories of copepods. *Frontiers in Ecology and Evolution* **6**, 23.

Huse, G., Strand, E. & Giske, J. (1999). Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evolutionary Ecology* **13**, 469–483.

Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, H. M., Bartholomae, C. H., van der Plas, A. K., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R. G., Lamont, T., Coetzee, J., Shillington, F., et al. (2009). The Benguela current: an ecosystem of four components. *Progress in Oceanography* **83**, 15–32.

Hutchinson, G. E. (1967). *A Treatise on Limnology. Introduction to Lake Biology and the Limnoplankton*. John Wiley and Sons, New York.

Ingvarsdóttir, A., Houlihan, D. F., Heath, M. R. & Hay, S. J. (1999). Seasonal changes in respiration rates of copepodite stage V *Calanus finmarchicus* (Gunnerus). *Fisheries Oceanography* **8**, 73–83.

Inoue, N., Saskai, T. & Oaki, R. (1953). "Kuroshio" undersea observation chamber. *Records of Oceanographic Works in Japan* **1**, 52–62.

Irigoien, X. (2004). Some ideas about the role of lipids in the life cycle of *Calanus finmarchicus*. *Journal of Plankton Research* **26**, 259–263.

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

Isaacs, J. D., Tont, S. A. & Wick, G. L. (1974). Deep scattering layers: vertical migration as a tactic for finding food. *Deep Sea Research and Oceanographic Abstracts* **21**, 651–656.

Ishii, M., Murase, H., Fukuda, Y., Sawada, K., Sasakura, T., Tamura, T., Bando, T., Matsuoka, K., Shinohara, A. & Nakatsuka, S. (2017). Diving behavior of sei whales *Balaenoptera borealis* relative to the vertical distribution of their potential prey. *Mammal Study* **42**, 191–199.

Iwasa, Y. (1982). Vertical migration of zooplankton: a game between predator and prey. *The American Naturalist* **120**, 171–180.

Jarnagin, S. T., Swan, B. K. & Kerfoot, W. C. (2000). Fish as vectors in the dispersal of *Bythotrephes cederstroemi*: diapausing eggs survive passage through the gut. *Freshwater Biology* **43**, 579–589.

Johnsen, G. H. & Jakobsen, P. J. (1987). The effect of food limitation on vertical migration in *Daphnia longispina*. *Limnology and Oceanography* **32**, 873–880.

Johnson, C. L., Leising, A. W., Runge, J. A., Head, E. J. H., Pepin, P., Plourde, S. & Durbin, E. G. (2008). Characteristics of *Calanus finmarchicus* dormancy patterns in the Northwest Atlantic. *ICES Journal of Marine Science* **65**, 339–350.

Johnson, M. W. (1948). Sound as a tool in marine ecology, from data on biological noises and the deep scattering layer. *Journal of Marine Research* **7**, 443–458.

Johnson, P. T., Stanton, D. E., Forshay, K. J. & Calhoun, D. M. (2018). Vertically challenged: how disease suppresses *Daphnia* vertical migration behavior. *Limnology and Oceanography* **63**, 886–896.

Jónasdóttir, S. H., Visser, A. W., Richardson, K. & Heath, M. R. (2015). Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 12122–12126.

Jónasdóttir, S. H., Wilson, R. J., Gislason, A. & Heath, M. R. (2019). Lipid content in overwintering *Calanus finmarchicus* across the subpolar eastern North Atlantic Ocean. *Limnology and Oceanography* **64**, 2029–2043.

Jones, C., Morozov, A. & Manley, J. E. (2013). Under ice positioning and communications for unmanned vehicles. In *Proceedings of the Oceans'13 MTS/IEEE Bergen Conference September 23–27, 2013*, pp. 1–6. IEEE, New York.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Juday, C. (1916). Limnological apparatus. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* **18**, 566–592.

Juday, C. (1926). A third report on limnological apparatus. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* **22**, 299–314.

Kaartvedt, S. (1996). Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. *Ophelia* **44**, 145–156.

Kaartvedt, S. (2000). Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. *ICES Journal of Marine Science* **57**, 1819–1824.

Kahn, R. E. & Lavery, A. C. (2019). Broadband acoustic quantification of mesopelagic zooplankton. *The Journal of the Acoustical Society of America* **146**, 2899–2899.

Kampa, E. M. (1975). Observations of a sonic-scattering layer during the total solar eclipse 30 June, 1973. *Deep Sea Research and Oceanographic Abstracts* **22**, 417–423.

Katija, K. & Dabiri, J. O. (2009). A viscosity-enhanced mechanism for biogenic ocean mixing. *Nature* **460**, 624–626.

Kenney, R. D., Hyman, M. A., Owen, R. E., Scott, G. P. & Winn, H. E. (1986). Estimation of prey densities required by western North Atlantic right whales. *Marine Mammal Science* **2**, 1–13.

Kessler, K., Lockwood, R. S., Williamson, C. E. & Saros, J. E. (2008). Vertical distribution of zooplankton in subalpine and alpine lakes: ultraviolet radiation, fish predation, and the transparency-gradient hypothesis. *Limnology and Oceanography* **53**, 2374–2382.

Kimmerer, W. J., Burau, J. & Bennett, W. (1998). Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnology and Oceanography* **43**, 1697–1709.

Kimmerer, W. J. & McKinnon, A. (1987). Zooplankton in a marine bay. II. Vertical migration to maintain horizontal distributions. *Marine Ecology Progress Series* **41**, 53–60.

Klyashtorin, L. & Yarzhomb, A. (1973). Energy consumption in active movements of planktonic organisms. *Oceanology-USSR* **13**, 575–580.

Kobari, T., Shinada, A. & Tsuda, A. (2003). Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific. *Progress in Oceanography* **57**, 279–298.

Kobari, T., Steinberg, D. K., Ueda, A., Tsuda, A., Silver, M. W. & Kitamura, M. (2008). Impacts of ontogenetically migrating copepods on downward carbon flux in the western subarctic Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* **55**, 1648–1660.

Kosobokova, K. N. (1999). The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. *Polar Biology* **22**, 254–263.

Koulouri, P., Dounas, C., Radin, F. & Eleftheriou, A. (2009). Near-bottom zooplankton in the continental shelf and upper slope of Heraklion Bay (Crete, Greece, eastern Mediterranean): observations on vertical distribution patterns. *Journal of Plankton Research* **31**, 753–762.

Kralj-Fišer, S. & Schuett, W. (2014). Studying personality variation in invertebrates: why bother? *Animal Behaviour* **91**, 41–52.

Kunze, E., Dower, J. F., Beveridge, I., Dewey, R. & Bartlett, K. P. (2006). Observations of biologically generated turbulence in a coastal inlet. *Science* **313**, 1768–1770.

Kuo-Cheng Shan, R. (1974). Reproduction in laboratory stocks of Pleuroxus (Chydoridae, Cladocera) under the influence of photoperiod and light intensity. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **59**, 643–666.

Kvile, K. Ø., Ashjian, C. J. & Ji, R. (2019). Pan-Arctic depth distribution of Diapausing Calanus copepods. *The Biological Bulletin* **237**, 76–89.

Kyba, C. C., Ruhtz, T., Fischer, J. & Hölker, F. (2011). Cloud coverage acts as an amplifier for ecological light pollution in urban ecosystems. *PLoS One* **6**, e17307.

L'Abée-Lund, J. H. & Vøllestad, L. A. (1987). Feeding migration of roach, *Rutilus rutilus* (L.), in Lake Arungen, Norway. *Journal of Fish Biology* **30**, 349–355.

Lacoursière-Roussel, A., Rosabal, M. & Bernatchez, L. (2016). Estimating fish abundance and biomass from eDNA concentrations: variability among capture methods and environmental conditions. *Molecular Ecology Resources* **16**, 1401–1414.

Lalli, C. & Parsons, T. (1993). *Biological Oceanography: An Introduction*. Elsevier Butturworth-Heinemann, Burlington.

Lampert, W. (1987). Vertical migration of freshwater zooplankton: indirect effects of vertebrate predators on algal communities. In *Predation: Direct and Indirect Impacts on Aquatic Communities* (eds W. C. Kerfoot and A. Sih), pp. 291–299. University Press of New England, Hanover.

Lampert, W. (1993). Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Archiv Für Hydrobiologie Ergebnisse der Limnologie* **39**, 79–88.

Lampert, W. & Loose, C. J. (1992). Plankton towers: bridging the gap between laboratory and field experiments. *Archiv Für Hydrobiologie Ergebnisse der Limnologie* **126**, 53–66.

Lampert, W. & Taylor, B. E. (1985). Zooplankton grazing in a eutrophic lake: implications of diel vertical migration. *Ecology* **66**, 68–82.

Lance, J. (1962). Effects of water of reduced salinity on the vertical migration of zooplankton. *Journal of the Marine Biological Association of the United Kingdom* **42**, 131–154.

Langbehn, T. J. & Varpe, Ø. (2017). Sea-ice loss boosts visual search: fish foraging and changing pelagic interactions in polar oceans. *Global Change Biology* **23**, 5318–5330.

Lansbury, I. (1955). Some notes on invertebrates other than Insecta found attached to water bugs (Hemipt.-Heteroptera). *Entomologiste* **88**, 139–140.

Lard, M., Bäckman, J., Yakovleva, M., Danielsson, B. & Hansson, L.-A. (2010). Tracking the small with the smallest–using nanotechnology in tracking zooplankton. *PLoS One* **5**, e13516.

Larson, R. & Harbison, G. (1989). Source and fate of lipids in polar gelatinous zooplankton. *Arctic* **42**, 339–346.

Larsson, P. & Lampert, W. (2011). Experimental evidence of a low-oxygen refuge for large zooplankton. *Limnology and Oceanography* **56**, 1682–1688.

Lass, S. & Spaak, P. (2003). Chemically induced anti-predator defences in plankton: a review. *Hydrobiologia* **491**, 221–239.

Last, K. S., Hobbs, L., Berge, J., Brierley, A. S. & Cottier, F. R. (2016). Moonlight drives ocean-scale mass vertical migration of zooplankton during the Arctic winter. *Current Biology* **26**, 244–251.

Latta, L. C. IV, O'Donnell, R. P. & Pfrender, M. E. (2009). Vertical distribution of *Chlamydomonas* changes in response to grazer and predator kairomones. *Oikos* **118**, 853–858.

Lavery, A. C. & Stanton, T. K. (2016). Broadband active acoustics for synoptic studies of marine ecosystem. *The Journal of the Acoustical Society of America* **139**, 2173–2173.

Lavery, A. C., Wiebe, P. H., Stanton, T. K., Lawson, G. L., Benfield, M. C. & Copley, N. J. (2007). Determining dominant scatterers of sound in mixed zooplankton populations. *The Journal of the Acoustical Society of America* **122**, 3304–3326.

Leach, T. H., Williamson, C. E., Theodore, N., Fischer, J. M. & Olson, M. H. (2015). The role of ultraviolet radiation in the diel vertical migration of zooplankton: an experimental test of the transparency-regulator hypothesis. *Journal of Plankton Research* **37**, 886–896.

Lee, R. F. (1975). Lipids of Arctic zooplankton. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry* **51**, 263–266.

Lee, R. F., Hagen, W. & Kattner, G. (2006). Lipid storage in marine zooplankton. *Marine Ecology Progress Series* **307**, 273–306.

Lee, W.-J., Chu, D. & Dosso, S. E. (2019). How much more informative are broadband compared to narrowband echoes for biological interpretation? *The Journal of the Acoustical Society of America* **146**, 2899.

Leech, D. M. & Williamson, C. E. (2001). *In situ* exposure to ultraviolet radiation alters the depth distribution of *Daphnia*. *Limnology and Oceanography* **46**, 416–420.

Levey, D. J. & Stiles, F. G. (1992). Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds. *The American Naturalist* **140**, 447–476.

Levy, D. A. (1990). Reciprocal diel vertical migration behavior in planktivores and zooplankton in British Columbia lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1755–1764.

Li, C., Sun, S., Wang, R. & Wang, X. (2004). Feeding and respiration rates of a planktonic copepod (*Calanus sinicus*) oversummering in Yellow Sea cold bottom waters. *Marine Biology* **145**, 149–157.

Lin, C. & Todo, T. (2005). The cryptochromes. *Genome Biology* **6**, 220–229.

Lindley, J. (1990). Distribution of overwintering calanoid copepod eggs in sea-bed sediments around southern Britain. *Marine Biology* **104**, 209–217.

Lischka, S. & Hagen, W. (2005). Life histories of the copepods *Pseudocalanus minutus*, *P. acuspes* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). *Polar Biology* **28**, 910–921.

Lock, A. R. & McLaren, I. A. (1970). The effect of varying and constant temperatures on the size of a marine copepod. *Limnology and Oceanography* **15**, 638–640.

Longhurst, A. R. (1967). Vertical distribution of zooplankton in relation to the eastern Pacific oxygen minimum. *Deep Sea Research and Oceanographic Abstracts* **14**, 51–63.

Longhurst, A. R. & Glen Harrison, W. (1989). The biological pump: profiles of plankton production and consumption in the upper ocean. *Progress in Oceanography* **22**, 47–123.

Longhurst, A. R., Reith, A., Bower, R. & Seibert, D. (1966). A new system for the collection of multiple serial plankton samples. *Deep Sea Research and Oceanographic Abstracts* **13**, 213–222.

Longhurst, A. R., Sameoto, D. D. & Herman, A. W. (1984). Vertical distribution of Arctic zooplankton in summer: eastern Canadian archipelago. *Journal of Plankton Research* **6**, 137–168.

Longhurst, A. R. & Williams, R. (1992). Carbon flux by seasonal vertical migrant copepods is a small number. *Journal of Plankton Research* **14**, 1495–1509.

Loose, C. J. & Dawidowicz, P. (1994). Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology* **75**, 2255–2263.

Ludvigsen, M., Berge, J., Geoffroy, M., Cohen, J. H., Pedro, R., Nornes, S. M., Singh, H., Sørensen, A. J., Daase, M. & Johnsen, G. H.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(2018). Use of an autonomous surface vehicle reveals small-scale diel vertical migrations of zooplankton and susceptibility to light pollution under low solar irradiance. *Science Advances* **4**, eaap9887.

Lundberg, M., Hop, H., Eiane, K., Gulliksen, B. & Falk-Petersen, S. (2006). Population structure and accumulation of lipids in the ctenophore *Mertensia ovum*. *Marine Biology* **149**, 1345–1353.

Lürling, M., Roozen, F., van Donk, E. & Goser, B. (2003). Response of *Daphnia* to substances released from crowded congeners and conspecifics. *Journal of Plankton Research* **25**, 967–978.

Maas, A. E., Blanco-Bercial, L., Lo, A., Tarrant, A. M. & Timmins-Schiffman, E. (2018). Variations in copepod proteome and respiration rate in association with Diel vertical migration and circadian cycle. *The Biological Bulletin* **235**, 30–42.

Macdonald, R. (1927). Food and habits of *Meganyctiphanes norvegica*. *Journal of the Marine Biological Association of the United Kingdom* **14**, 753–784.

Mack, H. R., Conroy, J. D., Blocksom, K. A., Stein, R. A. & Ludsin, S. A. (2012). A comparative analysis of zooplankton field collection and sample enumeration methods. *Limnology and Oceanography: Methods* **10**, 41–53.

Mackintosh, N. A. (1937). The seasonal circulation of the Antarctic macroplankton. *Discovery Reports* **16**, 365–412.

Madhupratap, M., Nair, V. R., Nair, S. & Achuthankutty, C. (1981). Thermocline & zooplankton distribution. *Indian Journal of Marine Science* **10**, 262–265.

Madhupratap, M., Nehring, S. & Lenz, J. (1996). Resting eggs of zooplankton (Copepoda and Cladocera) from the Kiel Bay and adjacent waters (southwestern Baltic). *Marine Biology* **125**, 77–87.

Madin, L., Horgan, E., Gallager, S. M., Eaton, J. & Girard, A. (2006). LAPIS: a new imaging tool for macro-zooplankton. In *Proceedings of the OCEANS' 06 MTS/IEEE Boston Conference, September 18–22*, pp. 1–5. IEEE, New York.

Madsen, S., Nielsen, T. G. & Hansen, B. W. (2001). Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. *Marine Biology* **139**, 75–93.

Maier, G. (1990). Spatial distribution of resting stages, rate of emergence from diapause and times to adulthood and to the appearance of the first clutch in 3 species of cyclopoid copepods. *Hydrobiologia* **206**, 11–18.

Makabe, R., Hattori, H., Sampei, M., Darnis, G., Fortier, L. & Sasaki, H. (2016). Can sediment trap-collected zooplankton be used for ecological studies? *Polar Biology* **39**, 2335–2346.

Makarov, R. (1979). Larval distribution and reproductive ecology of *Thysanoessa macrura* (Crustacea: Euphausiacea) in the Scotia Sea. *Marine Biology* **52**, 377–386.

Mäkinen, K., Vuorinen, I. & Hänninen, J. (2017). Climate-induced hydrography change favours small-bodied zooplankton in a coastal ecosystem. *Hydrobiologia* **792**, 83–96.

Malone, C. R. (1965). Dispersal of plankton: rate of food passage in mallard ducks. *The Journal of Wildlife Management* **29**, 529–533.

Maps, F., Pershing, A. J. & Record, N. R. (2012a). A generalized approach for simulating growth and development in diverse marine copepod species. *ICES Journal of Marine Science* **69**, 370–379.

Maps, F., Record, N. R. & Pershing, A. J. (2013). A metabolic approach to dormancy in pelagic copepods helps explaining inter-and intra-specific variability in life-history strategies. *Journal of Plankton Research* **36**, 18–30.

Maps, F., Runge, J. A., Leising, A. W., Pershing, A. J., Record, N. R., Plourde, S. & Pierson, J. J. (2012b). Modelling the timing and duration of dormancy in populations of *Calanus finmarchicus* from the Northwest Atlantic shelf. *Journal of Plankton Research* **34**, 36–54.

Maps, F., Zakardjian, B. A., Plourde, S. & Saucier, F. J. (2011). Modeling the interactions between the seasonal and diel migration behaviors of *Calanus finmarchicus* and the circulation in the Gulf of St. Lawrence (Canada). *Journal of Marine Systems* **88**, 183–202.

Marcogliese, D. J. & Esch, G. W. (1992). Alterations of vertical distribution and migration of zooplankton in relation to temperature. *American Midland Naturalist* **128**, 139–155.

Marcus, N. H. (1980). Photoperiodic control of diapause in the marine calanoid copepod *Labidocera aestiva*. *The Biological Bulletin* **159**, 311–318.

Marcus, N. H. (1995). Seasonal study of planktonic copepods and their benthic resting eggs in northern California coastal waters. *Marine Biology* **123**, 459–465.

Marcus, N. H. (1996). Ecological and evolutionary significance of resting eggs in marine copepods: past, present, and future studies. *Hydrobiologia* **320**, 141–152.

Marcus, N. H. & Schmidt-Gengenbach, J. (1986). Recruitment of individuals into the plankton: the importance of bioturbation. *Limnology and Oceanography* **31**, 206–210.

Mariash, H. L., Cusson, M. & Rautio, M. (2017). Fall composition of storage lipids is associated with the overwintering strategy of *Daphnia*. *Lipids* **52**, 83–91.

Marshall, S. M. & Orr, A. P. (1972). *The Biology of a Marine Copepod: Calanus finmarchicus (Gunnerus)*. Springer Science & Business Media, Berlin.

Marta-Almeida, M., Dubert, J., Peliz, Á. & Queiroga, H. (2006). Influence of vertical migration pattern on retention of crab larvae in a seasonal upwelling system. *Marine Ecology Progress Series* **307**, 1–19.

Masson, S., Pinel-Alloul, B., Méthot, G. & Richard, N. (2004). Comparison of nets and pump sampling gears to assess zooplankton vertical distribution in stratified lakes. *Journal of Plankton Research* **26**, 1199–1206.

Maszczyk, P. (2016). Miniature plankton columns to study the depth distribution of zooplankton at gradients of food, predation risk, temperature, and UV radiation. *Limnology and Oceanography: Methods* **14**, 210–223.

Mauchline, J. (1998). *The Biology of Calanoid Copepods*. Academic Press, San Diego.

Maynard Smith, J. (1979). Game theory and the evolution of behaviour. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **205**, 475–488.

Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

McAllister, C. (1969). Aspects of estimating zooplankton production from phytoplankton production. *Journal of the Fisheries Board of Canada* **26**, 199–220.

McKinnon, L., Smith, P. A., Nol, E., Martin, J. L., Doyle, F. I., Abraham, K. F., Gilchrist, H. G., Morrison, R. I. G. & Bêty, J. (2010). Lower predation risk for migratory birds at high latitudes. *Science* **327**, 326–327.

McLaren, I. A. (1963). Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. *Journal of the Fisheries Research Board of Canada* **20**, 685–727.

McLaren, I. A. (1974). Demographic strategy of vertical migration by a marine copepod. *The American Naturalist* **108**, 91–102.

McManus, M. A. & Woodson, C. B. (2012). Plankton distribution and ocean dispersal. *Journal of Experimental Biology* **215**, 1008–1016.

McNaught, D. C. (1969). Developments in acoustic plankton sampling. In *Proceedings of the 12th Conference on Great Lakes Research*, pp. 61–68. Great Lakes Research Institute, Ann Arbor.

McQueen, D. J. & Yan, N. D. (1993). Metering filtration efficiency of freshwater zooplankton hauls: reminders from the past. *Journal of Plankton Research* **15**, 57–65.

Melle, W., Runge, J. A., Head, E. J. H., Plourde, S., Castellani, C., Licandro, P., Pierson, J., Jónasdóttir, S. H., Johnson, C. L. & Broms, C. (2014). The North Atlantic Ocean as habitat for *Calanus finmarchicus*: environmental factors and life history traits. *Progress in Oceanography* **129**, 244–284.

Mellors, W. K. (1975). Selective predation of ephippal *Daphnia* and the resistance of ephippal eggs to digestion. *Ecology* **56**, 974–980.

Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, G., Kofinas, A., Mackintosh, J., Melbourne-Thomas, M. M. C., Muelbert, G., Ottersen, H. P. & Schuur, E. A. G. (2019). Polar regions. In *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate* (eds H. Pörtner, D. Roberts, P. Masson-Delmotte, M. Zhai, E. Tignor, K. Poloczanska, A. Mintenbeck, M. Alegría, A. Nicolai, J. Okem, B. Petzold, B. Rama and N. Weyer), pp. 203–320. IPCC, Intergovernmental Panel on Climate Change, Geneva.

Merten, W., Appeldoorn, R., Rivera, R. & Hammond, D. (2014). Diel vertical movements of adult male dolphinfish (*Coryphaena hippurus*) in the western Central Atlantic as determined by use of pop-up satellite archival transmitters. *Marine Biology* **161**, 1823–1834.

Metz, C. (1995). Seasonal variation in the distribution and abundance of *Oithona* and *Oncaea* species (Copepoda, Crustacea) in the southeastern Weddell Sea, Antarctica. *Polar Biology* **15**, 187–194.

Meysman, F. J., Middelburg, J. J. & Heip, C. H. (2006). Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology & Evolution* **21**, 688–695.

Michael, E. L. R. (1911). *Classification and Vertical Distribution of the Chaetognatha of the San Diego Region: Including Redescriptions of Some Doubtful Species of the Group*. The University Press, California.

Miller, C. B., Cowles, T. J., Wiebe, P. H., Copley, N. J. & Grigg, H. (1991). Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms. *Marine Ecology Progress Series* **72**, 79–91.

Miller, C. B., Frost, B. W., Batchelder, H. P., Clemons, M. J. & Conway, R. E. (1984). Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. *Progress in Oceanography* **13**, 201–243.

Miller, D. (1961). A modification of the small Hardy plankton sampler for simultaneous high-speed plankton hauls. *Bulletin of Marine Ecology* **5**, 165–172.

Miner, B. E., de Meester, L., Pfrender, M. E., Lampert, W. & Hairston, N. G. (2012). Linking genes to communities and ecosystems: *Daphnia* as an ecogenomic model. *Proceedings of the Royal Society B: Biological Sciences* **279**, 1873–1882.

Møller, E. F. & Nielsen, T. G. (2020). Borealization of Arctic zooplankton—smaller and less fat zooplankton species in Disko Bay, Western Greenland. *Limnology and Oceanography* **65**, 1175–1188.

Moore, A. R. (1912). Concerning negative phototropism in *Daphnia pulex*. *Journal of Experimental Zoology* **13**, 573–575.

Moore, M. V., Pierce, S. M., Walsh, H. M., Kvalvik, S. K. & Lim, J. D. (2000). Urban light pollution alters the diel vertical migration of *Daphnia*. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen* **27**, 779–782.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Morgan, S. G. & Fisher, J. L. (2010). Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. *Marine Ecology Progress Series* **404**, 109–126.

Morris, M., Gust, G. & Torres, J. (1985). Propulsion efficiency and cost of transport for copepods: a hydromechanical model of crustacean swimming. *Marine Biology* **86**, 283–295.

Morton, K. & MacLellan, S. (1992). Acoustics and freshwater zooplankton. *Journal of Plankton Research* **14**, 1117–1125.

Motoda, S., Anraku, M. & Minoda, T. (1957). Experiments on the performance of plankton samplings with net. *Bulletin of the Faculty of Fisheries Hokkaido University* **8**, 1–22.

Mous, P., van Densen, W. & Machiels, M. (2004). Vertical distribution patterns of zooplanktivorous fish in a shallow, eutrophic lake, mediated by water transparency. *Ecology of Freshwater Fish* **13**, 61–69.

Muluk, C. B. & Bekliogl u, M. (2005). Absence of typical diel vertical migration in *Daphnia*: varying role of water clarity, food, and dissolved oxygen in Lake Eymir, Turkey. *Hydrobiologia* **537**, 125–133.

Musyl, M. K., Brill, R. W., Boggs, C. H., Curran, D. S., Kazama, T. K. & Seki, M. P. (2003). Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian islands from archival tagging data. *Fisheries Oceanography* **12**, 152–169.

Myrberg, J. & Arthur, A. (1973). Underwater television—a tool for the marine biologist. *Bulletin of Marine Science* **23**, 824–836.

Næss, T. & Nilssen, J. P. (1991). Diapausing fertilized adults. *Oecologia* **86**, 368–371.

Narver, D. W. (1970). Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. *Journal of the Fisheries Board of Canada* **27**, 281–316.

Neill, W. E. (1990). Induced vertical migration in copepods as a defence against invertebrate predation. *Nature* **345**, 524–526.

Nelson, D. R., McKibben, J. N., Strong, W. R., Lowe, C. G., Sisneros, J. A., Schroeder, D. M. & Lavenberg, R. J. (1997). An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes* **49**, 389–399.

Nishizawa, S., Fukuda, M. & Inoue, N. (1954). Photographic study of suspended matter and plankton in the sea. *Bulletin of the Faculty of Fisheries Hokkaido University* **5**, 36–40.

Norrbin, F. (1996). Timing of diapause in relation to the onset of winter in the high-latitude copepods *Pseudocalanus acuspes* and *Acartia longiremis*. *Marine Ecology Progress Series* **142**, 99–109.

Novikova, N., Gusev, O., Polikarpov, N., Deshevaya, E., Levinskikh, M., Alekseev, V., Okuda, T., Sugimoto, M., Sychev, V. & Grigoriev, A. (2011). Survival of dormant organisms after long-term exposure to the space environment. *Acta Astronautica* **68**, 1574–1580.

Ogram, A., Sayler, G. S. & Barkay, T. (1987). The extraction and purification of microbial DNA from sediments. *Journal of Microbiological Methods* **7**, 57–66.

Ohman, M. D. (1990). The demographic benefits of diel vertical migration by zooplankton. *Ecological Monographs* **60**, 257–281.

Ohman, M. D., Davis, R. E., Sherman, J. T., Grindley, K. R., Whitmore, B. M., Nickels, C. F. & Ellen, J. S. (2019). Zooglider: an autonomous vehicle for optical and acoustic sensing of zooplankton. *Limnology and Oceanography: Methods* **17**, 69–86.

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

Ohman, M. D. & Romagnan, J. B. (2016). Nonlinear effects of body size and optical attenuation on Diel vertical migration by zooplankton. *Limnology and Oceanography* **61**, 765–770.

Ohman, M. D., Rudnick, D. L., Chekalyuk, A., Davis, R. E., Feely, R. A., Kahru, M., Kim, H.-J., Landry, M. R., Martz, T. R. & Sabine, C. L. (2013). Autonomous Ocean measurements in the California current ecosystem. *Oceanography* **26**, 18–25.

Onbé, T. (1991). Some aspects of the biology of resting eggs of marine cladocerans. *Crustacean Egg Production* **41**, 1–3.

Onsrud, M. S. & Kaartvedt, S. (1998). Diel vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. *Marine Ecology Progress Series* **171**, 209–219.

Opdal, A. F., Lindemann, C. & Aksnes, D. L. (2019). Centennial decline in North Sea water clarity causes strong delay in phytoplankton bloom timing. *Global Change Biology* **25**, 3946–3953.

Orcutt, J. D. & Porter, K. G. (1983). Diel vertical migration by zooplankton: constant and fluctuating temperature effects on life history parameters of *Daphnia*. *Limnology and Oceanography* **28**, 720–730.

Osgood, K. E. & Frost, B. W. (1994). Ontogenetic diel vertical migration behaviors of the marine planktonic copepods *Calanus pacificus* and *Metridia lucens*. *Marine Ecology Progress Series* **104**, 13–25.

Østvedt, O. J. (1955). Zooplankton investigations from weather ship M in the Norwegian Sea, 1948-49. *Hvalrådets Skrifter* **40**, 1–93.

Ostwald, W. (1902). Theorie des Planktons. *Biologisches Zentralblatt* **22**, 596–605.

Owens, J. D., Houston, M., Luebke, D., Green, S., Stone, J. E. & Phillips, J. C. (2008). GPU computing. *Proceedings of the IEEE* **96**, 879–899.

Pancella, J. R. & Stross, R. G. (1963). Light induced hatching of *Daphnia* resting eggs. *Chesapeake Science* **4**, 135–140.

Parker, G. H. (1902). The reactions of copepods to various stimuli and the bearing of this on daily depth-migrations. *Bulletin of United States Fish Commission* **22**, 103–123.

Pasternak, A. F. & Arashkevich, E. (1999). Resting stages in the life cycle of *Eudiaptomus graciloides* (Lill.)(Copepoda: Calanoida) in Lake Glubokoe. *Journal of Plankton Research* **21**, 309–325.

Patalas, K. (1954). Comparative studies on a new type of self acting water sampler for plankton and hydrochemical investigations. *Ekologia Polska* **2**, 231–242.

Pearre, S. (1979). Problems of detection and interpretation of vertical migration. *Journal of Plankton Research* **1**, 29–44.

Pearre, S. (2003). Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biological Reviews* **78**, 1–79.

Pedersen, G., Falk-Petersen, S., Dunlop, K., Camus, L., Daase, M., Basedow, S. L., Bandara, K., Tverberg, V., Pederick, J. & Peddie, D. (2019). Autonomous surface vehicles for persistent acoustic monitoring of zooplankton in a highly productive shelf area. In *Proceedings of the OCEANS'19 MTS/IEEE Marseille Conference, October 27–31*, pp. 1–7. IEEE, New York.

Pedersen, G., Tande, K. S. & Ottesen, G. (1995). Why does a component of *Calanus finmarchicus* stay in the surface waters during the overwintering period in high latitudes? *ICES Journal of Marine Science* **52**, 523–531.

Pedersen, O. P., Gaardsted, F., Lågstad, P. & Tande, K. S. (2010). On the use of the HUGIN 1000 HUS autonomous underwater vehicle for high resolution zooplankton measurements. *Journal of Operational Oceanography* **3**, 17–25.

Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915.

Petersen, W. (2014). FerryBox systems: state-of-the-art in Europe and future development. *Journal of Marine Systems* **140**, 4–12.

Petersen, W., Petschatnikov, M., Schroeder, F. & Colijn, F. (2003). FerryBox systems for monitoring coastal waters. In *Elsevier Oceanography Series* (eds H. Dahlin, N. C. Flemming, K. Nittis and S. E. Petersson), pp. 325–333. Elsevier, Amsterdam.

Peterson, W. T. (1998). Life cycle strategies of copepods in coastal upwelling zones. *Journal of Marine Systems* **15**, 313–326.

Peterson, W. T., Miller, C. B. & Hutchinson, A. (1979). Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep Sea Research Part A. Oceanographic Research Papers* **26**, 467–494.

Petipa, T. (1966). On the energy balance of *Calanus helgolandicus* (Claus) in the Black Sea. In *Physiology of Marine Animals* (ed. V. S. Ivlev), pp. 60–81. Academy of Science USSR, Moscow.

Petipa, T. & Makarova, N. (1969). Dependence of phytoplankton production on rhythm and rate of elimination. *Marine Biology* **3**, 191–195.

Petiver, J. (1704). *Gazophylacium naturae et artis*. Smith & Bateman, London.

Petrusevich, V., Dmitrenko, I. A., Kirillov, S. A., Rysgaard, S., Falk-Petersen, S., Barber, D. G., Boone, W. & Ehn, J. K. (2016). Wintertime water dynamics and moonlight disruption of the acoustic backscatter diurnal signal in an ice-covered Northeast Greenland fjord. *Journal of Geophysical Research: Oceans* **121**, 4804–4818.

Petzoldt, T., Rudolf, L., Rinke, K. & Benndorf, J. (2009). Effects of zooplankton diel vertical migration on a phytoplankton community: a scenario analysis of the underlying mechanisms. *Ecological Modelling* **220**, 1358–1368.

Picapedra, P., Lansac-Tôha, F. & Bialetzki, A. (2015). Diel vertical migration and spatial overlap between fish larvae and zooplankton in two tropical lakes, Brazil. *Brazilian Journal of Biology* **75**, 352–361.

Pijanowska, J. & Dawidowicz, P. (1987). The lack of vertical migration in *Daphnia*: the effect of homogenously distributed food. *Hydrobiologia* **148**, 175–181.

Pijanowska, J. & Stolpe, G. (1996). Summer diapause in *Daphnia* as a reaction to the presence of fish. *Journal of Plankton Research* **18**, 1407–1412.

Pillar, S., Armstrong, D. & Hutchings, L. (1989). Vertical migration, dispersal and transport of *Euphausia lucens* in the southern Benguela current. *Marine Ecology Progress Series* **53**, 179–190.

Pinti, J. & Visser, A. W. (2019). Predator-prey games in multiple habitats reveal mixed strategies in Diel vertical migration. *The American Naturalist* **193**, E65–E77.

Piscia, R., Tabozzi, S., Bettinetti, R., Nevalainen, L. & Manca, M. M. (2016). Unexpected increases in rotifer resting egg abundances during the period of contamination of Lake Orta. *Journal of Limnology* **75**, 76–85.

Plourde, S., Joly, P., Runge, J. A., Dodson, J. & Zakardjian, B. A. (2003). Life cycle of *Calanus hyperboreus* in the lower St. Lawrence estuary and its relationship to local environmental conditions. *Marine Ecology Progress Series* **255**, 219–233.

Pond, D. W. & Tarling, G. A. (2011). Phase transitions of wax esters adjust buoyancy in diapausing *Calanoides acutus*. *Limnology and Oceanography* **56**, 1310–1318.

Pond, D. W. & Tarling, G. A. (2013). Solid evidence or fluid ideas on the importance lipid phase transitions to diapausing copepods: reply. *Journal of Plankton Research* **35**, 441–443.

Pond, D. W., Tarling, G. A., Ward, P. & Mayor, D. J. (2012). Wax ester composition influences the diapause patterns in the copepod *Calanoides acutus*. *Deep Sea Research Part II: Topical Studies in Oceanography* **59**, 93–104.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Pourriot, R. & Snell, T. W. (1983). Resting eggs in rotifers. In *Biology of Rotifers* (eds P. R. Birger and S. T. Nogrady), pp. 213–224. Springer, Dordrecht.

Powell, J. R. & Ohman, M. D. (2012). Use of glider-class acoustic Doppler profilers for estimating zooplankton biomass. *Journal of Plankton Research* **34**, 563–568.

Prairie, J. C., Sutherland, K. R., Nickols, K. J. & Kaltenberg, A. M. (2012). Biophysical interactions in the plankton: a cross-scale review. *Limnology and Oceanography: Fluids and Environments* **2**, 121–145.

Proctor, V. W., Malone, C. R. & DeVlaming, V. L. (1967). Dispersal of aquatic organisms: viability of disseminules recovered from the intestinal tract of captive killdeer. *Ecology* **48**, 672–676.

Pu, X.-M., Sun, S., Yang, B., Zhang, G.-T. & Zhang, F. (2004). Life history strategies of *Calanus sinicus* in the southern Yellow Sea in summer. *Journal of Plankton Research* **26**, 1059–1068.

Purcell, J. E., Hopcroft, R. R., Kosobokova, K. N. & Whitledge, T. E. (2010). Distribution, abundance, and predation effects of epipelagic ctenophores and jellyfish in the western Arctic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* **57**, 127–135.

Radzikowski, J. (2013). Resistance of dormant stages of planktonic invertebrates to adverse environmental conditions. *Journal of Plankton Research* **35**, 707–723.

Ramacharan, C. W. & Sprules, W. G. (1989). Preliminary results from an inexpensive motion analyzer for free-swimming zooplankton. *Limnology and Oceanography* **34**, 457–462.

Record, N. R., Ji, R., Maps, F., Varpe, Ø., Runge, J. A., Petrik, C. M. & Johns, D. (2018). Copepod diapause and the biogeography of the marine lipidscape. *Journal of Biogeography* **45**, 2238–2251.

Reede, T. & Ringelberg, J. (1995). The influence of a fish exudate on two clones of the hybrid *Daphnia galeata×hyalina*. *Hydrobiologia* **307**, 207–212.

Reichwaldt, E. S. & Stibor, H. (2005). Effects of a fluctuating temperature regime experienced by *Daphnia* during diel vertical migration on *Daphnia* life history parameters. *Hydrobiologia* **543**, 199–205.

Reichwaldt, E. S., Wolf, I. D. & Stibor, H. (2004). The effect of different zooplankton grazing patterns resulting from diel vertical migration on phytoplankton growth and composition: a laboratory experiment. *Oecologia* **141**, 411–419.

Reif, C. B. & Tappa, D. W. (1966). Selective predation: smelt and cladocerans in Harveys Lake. *Limnology and Oceanography* **11**, 437–438.

Rey-Rassat, C., Irigoien, X., Harris, R. P. & Carlotti, F. (2002). Energetic cost of gonad development in *Calanus finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series* **238**, 301–306.

Rhode, S. C., Pawlowski, M. & Tollrian, R. (2001). The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. *Nature* **412**, 69–72.

Ricci, C. (2001). Dormancy patterns in rotifers. *Hydrobiologia* **446**, 1–11.

Richter, C. (1995). Seasonal changes in the vertical distribution of mesozooplankton in the Greenland Sea gyre (75° N): distribution strategies of calanoid copepods. *ICES Journal of Marine Science* **52**, 533–539.

Ringelberg, J. (1964). The positively phototactic reaction of *Daphnia magna* Straus: a contribution to the understanding of diurnal vertical migration. *Netherlands Journal of Sea Research* **2**, 319–406.

Ringelberg, J. (1995a). An account of a preliminary mechanistic model of swimming behaviour in *Daphnia*: its use in understanding diel vertical migration. In *Cladocera as Model Organisms in Biology* (eds P. Larsson and L. J. Weider), pp. 161–165. Kluwer Academic Publishers, Dordrecht.

Ringelberg, J. (1995b). 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**, 15–25.

Ringelberg, J. (1999). The photobehaviour of *Daphnia* spp. as a model to explain diel vertical migration in zooplankton. *Biological Reviews* **74**, 397–423.

Ringelberg, J. & Servaas, H. (1971). A circadian rhythm in *Daphnia magna*. *Oecologia* **6**, 289–292.

Ringelberg, J. & van Gool, E. (2003). On the combined analysis of proximate and ultimate aspects in diel vertical migration (DVM) research. *Hydrobiologia* **491**, 85–90.

Robin, W. B., Borsani, J. F., Hanson, M. B. & Peter, L. T. (2002). Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. *Marine Ecology Progress Series* **237**, 301–305.

Rodríguez, J. M., Cabrero, A., Gago, J., Guevara-Fletcher, C., Herrero, M., Hernandez de Rojas, A., Garcia, A., Laiz-Carrion, R., Vergara, A. & Alvarez, P. (2015). Vertical distribution and migration of fish larvae in the NW Iberian upwelling system during the winter mixing period: implications for cross-shelf distribution. *Fisheries Oceanography* **24**, 274–290.

Rossi, V., Albini, D., Benassi, G. & Menozzi, P. (2012). To rest in hydration: hatching phenology of resting eggs of *Heterocypris incongruens* (Crustacea: Ostracoda). *Fundamental and Applied Limnology/Archiv für Hydrobiologie* **181**, 49–58.

Rudjakov, J. (1970). The possible causes of diel vertical migrations of planktonic animals. *Marine Biology* **6**, 98–105.

Russell, F. S. (1926). The vertical distribution of marine macroplankton IV. The apparent importance of light intensity as a controlling factor in the behaviour of certain species in the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom* **14**, 415–440.

Russell, F. S. (1927). The vertical distribution of plankton in the sea. *Biological Reviews* **2**, 213–262.

Ruttner, F. (1953). *Fundamentals of Limnology; Translated to English by Frey, D.G and Fry, FEJ*. University of Toronto Press, Toronto.

Sainmont, J., Gislason, A., Heuschele, J., Webster, C. N., Sylvander, P., Wang, M. & Varpe, Ø. (2014). Inter-and intra-specific diurnal habitat selection of zooplankton during the spring bloom observed by video plankton recorder. *Marine Biology* **161**, 1931–1941.

Saito, H. & Hattori, H. (1997). Diel vertical migration and feeding rhythm of copepods under sea ice at Saroma-ko lagoon. *Journal of Marine Systems* **11**, 191–203.

Saito, H. & Kiørboe, T. (2001). Feeding rates in the chaetognath *Sagitta elegans*: effects of prey size, prey swimming behaviour and small-scale turbulence. *Journal of Plankton Research* **23**, 1385–1398.

Sakshaug, E., Johnsen, G. H., Kristiansen, S., von Quillfeldt, C., Rey, F., Slagstad, D. & Thingstad, F. (2009). Phytoplankton and primary production. In *Ecosystem Barents Sea* (eds E. Sakshaug, G. H. Johnsen and K. M. Kovacs), pp. 167–209. Tapir Academic Press, Trondheim.

Samemoto, D. (1987). Vertical distribution and ecological significance of chaetognaths in the Arctic environment of Baffin Bay. *Polar Biology* **7**, 317–328.

Sameoto, D., Jaroszynski, L. & Fraser, W. (1980). BIONESS, a new design in multiple net zooplankton samplers. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 722–724.

Sancar, A. (2003). Structure and function of DNA photolyase and cryptochrome blue-light photoreceptors. *Chemical Reviews* **103**, 2203–2238.

Santer, B., Blohm-Sievers, E., Cáceres, C. E. & Hairston, N. G. (2000). Life-history variation in the coexisting freshwater copepods *Eudiaptomus gracilis* and *Eudiaptomus graciloides*. *Archiv Für Hydrobiologie Ergebnisse der Limnologie* **149**, 441–458.

Sartoris, F. J., Thomas, D. N., Cornils, A. & Schiela, S. B. S. (2010). Buoyancy and diapause in Antarctic copepods: the role of ammonium accumulation. *Limnology and Oceanography* **55**, 1860–1864.

Sarvala, J. (1979). Benthic resting periods of pelagic cyclopoids in an oligotrophic lake. *Ecography* **2**, 88–100.

Saumweber, W. J. & Durbin, E. G. (2006). Estimating potential diapause duration in *Calanus finmarchicus*. *Deep Sea Research Part II: Topical Studies in Oceanography* **53**, 2597–2617.

Scharfenberg, U. (1910). *Studien und experimente über die eibildung und den generationszyklus von Daphnia magna*. Verlag von Julius Klinkhardt, Berlin.

Schindler, D. (1969). Two useful devices for vertical plankton and water sampling. *Journal of the Fisheries Board of Canada* **26**, 1948–1955.

Schmid, M. S., Maps, F. & Fortier, L. (2018). Lipid load triggers migration to diapause in Arctic *Calanus* copepods—insights from underwater imaging. *Journal of Plankton Research* **40**, 311–325.

Schmidt, K. (2010). Food and feeding in northern krill (*Meganyctiphanes norvegica* Sars). In *Advances in Marine Biology* (ed. G. A. Tarling), pp. 127–171. Academic Press, London.

Schmidtlein, R. (1879). Vergleichende Übersicht über das Erscheinen gröfserer pelagischer Thiere und Bemerkungen über Fortpflan-zungsverhältnisse einiger Seethiere im Aquarium. *Mittheilungen aus der Zoologischen Station zu Neapel* **2**, 162–175.

Schmitt, F. G. & Seuront, L. (2001). Multifractal random walk in copepod behavior. *Physica A: Statistical Mechanics and its Applications* **301**, 375–396.

Schnack-Schiel, S. B. (2001). Aspects of the study of the life cycles of Antarctic copepods. *Hydrobiologia* **453**, 9–24.

Schnack-Schiel, S. B. & Hagen, W. (1994). Life cycle strategies and seasonal variations in distribution and population structure of four dominant calanoid copepod species in the eastern Weddell Sea, Antarctica. *Journal of Plankton Research* **16**, 1543–1566.

Schnack-Schiel, S. B. & Hagen, W. (1995). Life-cycle strategies of *Calanoides acutus*, *Calanus propinquus*, *and Metridia gerlachei* (Copepoda: Calanoida) in the eastern Weddell Sea, Antarctica. *ICES Journal of Marine Science* **52**, 541–548.

Schnack-Schiel, S. B., Hagen, W. & Mizdalski, E. (1991). Seasonal comparison of *Calanoides acutus* and *Calanus propinquus*(Copepoda: Calanoida) in the southeastern Weddell Sea, Antarctica. *Marine Ecology Progress Series* **70**, 17–27.

Schneider, T., Grosbois, G., Vincent, W. F. & Rautio, M. (2016). Carotenoid accumulation in copepods is related to lipid metabolism and reproduction rather than to UV-protection. *Limnology and Oceanography* **61**, 1201–1213.

Schneider, T., Grosbois, G., Vincent, W. F. & Rautio, M. (2017). Saving for the future: pre-winter uptake of algal lipids supports copepod egg production in spring. *Freshwater Biology* **62**, 1063–1072.

Schwartz, S. S. & Hebert, P. D. N. (1987). Methods for the activation of the resting eggs of *Daphnia*. *Freshwater Biology* **17**, 373–379.

Seear, P., Tarling, G. A., Teschke, M., Meyer, B., Thorne, M. A. S., Clark, M. S., Gaten, E. & Rosato, E. (2009). Effects of simulated light regimes

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

on gene expression in Antarctic krill (*Euphausia superba* Dana). *Journal of Experimental Marine Biology and Ecology* **381**, 57–64.

Sekino, T. & Yamamura, N. (1999). Diel vertical migration of zooplankton: optimum migrating schedule based on energy accumulation. *Evolutionary Ecology* **13**, 267–282.

Sell, A. F. (1998). Adaptation to oxygen deficiency: contrasting patterns of haemoglobin synthesis in two coexisting *Daphnia* species. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **120**, 119–125.

Sentyabov, E. & Prokopchuk, I. (2006). Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. *ICES Journal of Marine Science* **63**, 117–127.

Shan, R. K. C. (1970). Influence of light on hatching resting eggs of chydorids (Cladocera). *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **55**, 295–302.

Shepard, E. L., Ahmed, M. Z., Southall, E. J., Witt, M. J., Metcalfe, J. D. & Sims, D. W. (2006). Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecology Progress Series* **328**, 205–213.

Sherman, K. & Honey, K. A. (1970). Vertical movements of zooplankton during a solar eclipse. *Nature* **227**, 1156–1158.

Shokralla, S., Spall, J. L., Gibson, J. F. & Hajibabaei, M. (2012). Next-generation sequencing technologies for environmental DNA research. *Molecular Ecology* **21**, 1794–1805.

Sieburth, J. M. N., Smetacek, V. & Lenz, J. (1978). Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnology and Oceanography* **23**, 1256–1263.

Sieracki, M. E., Benfield, M. C., Hanson, A., Davis, C. S., Pilskaln, C. H., Checkley, D., Sosik, H. M., Ashjian, C. J., Culverhouse, P. & Cowen, R. (2010). Optical plankton imaging and analysis systems for ocean observation. In *Proceedings of Ocean OceanObs'09: Sustained Ocean Observations and Information for Society* (eds J. Hall, D. E. Harrison and D. Stammerpp), pp. 21–25. ESA Publications, Venice.

Siferd, T. D. & Conover, R. J. (1992). Natural history of ctenophores in the resolute passage area of the Canadian high Arctic with special reference to *Mertensia ovum*. *Marine Ecology Progress Series* **86**, 133–144.

Sims, D. W., Southall, E. J., Richardson, A. J., Reid, P. C. & Metcalfe, J. D. (2003). Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series* **248**, 187–196.

Sims, D. W., Southall, E. J., Tarling, G. A. & Metcalfe, J. D. (2005). Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology* **74**, 755–761.

Skaret, G., Johansen, G. O., Johnsen, E., Fall, J., Fiksen, Ø., Englund, G., Fauchald, P., Gjøsæter, H., Macaulay, G. J. & Johannesen, E. (2020). Diel vertical movements determine spatial interactions between cod, pelagic fish and krill on an Arctic shelf bank. *Marine Ecology Progress Series* **638**, 13–23.

Skjoldal, H. R., Wiebe, P. H., Postel, L., Knutsen, T., Kaartvedt, S. & Sameoto, D. D. (2013). Intercomparison of zooplankton (net) sampling systems: results from the ICES/GLOBEC Sea-going workshop. *Progress in Oceanography* **108**, 1–42.

Skottene, E., Tarrant, A. M., Olsen, A. J., Altin, D., Østensen, M.-A., Hansen, B. H., Choquet, M., Jenssen, B. M. & Olsen, R. E. (2019). The β-oxidation pathway is downregulated during diapause termination in *Calanus* copepods. *Scientific Reports* **9**, 1–13.

Slagstad, D. & Tande, K. S. (2007). Structure and resilience of overwintering habitats of *Calanus finmarchicus* in the eastern Norwegian Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* **54**, 2702–2715.

Ślusarczyk, M. (1995). Predator-induced diapause in *Daphnia*. *Ecology* **76**, 1008–1013.

Smith, C., Hill, A., Foreman, M. & Peña, M. (2001). Horizontal transport of marine organisms resulting from interactions between diel vertical migration and tidal currents off the west coast of Vancouver Island. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 736–748.

Smith, R. J. & Moore, F. R. (2005). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology* **57**, 231–239.

Smith, S. L., Pieper, R. E., Moore, M. V., Rudstam, L., Greene, C. H., Zamon, J. E., Flagg, C. N. & Williamson, C. E. (1992). Acoustic techniques for the *in-situ* observation of zooplankton. *Archiv Für Hydrobiologie Ergebnisse der Limnologie* **36**, 23–43.

Smyly, W. J. P. (1961). The life-cycle of the freshwater copepod *Cyclops leuckarti* Claus in Esthwaite water. *The Journal of Animal Ecology* **30**, 153–169.

Smyly, W. J. P. (1962). Laboratory experiments with stage V copepodids of the freshwater copepod, *Cyclops leuckarti* Claus, from Windermere and Esthwaite water. *Crustaceana* **4**, 273–280.

Snucins, E. & John, G. (2000). Interannual variation in the thermal structure of clear and colored lakes. *Limnology and Oceanography* **45**, 1639–1646.

Sømme, J. D. (1934). Animal plankton of the Norwegian coast waters and the open sea. I. Production of *Calanus finmarchicus* (gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten area. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* **4**, 1–163.

Søreide, J. E., Falk-Petersen, S., Hegseth, E. N., Hop, H., Carroll, M. L., Hobson, K. A. & Błachowiak-Samołyk, K. (2008). Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. *Deep Sea Research Part II: Topical Studies in Oceanography* **55**, 2225–2244.

Southwood, T. R. E. (1962). Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* **37**, 171–211.

Speekmann, C. L., Bollens, S. M. & Avent, S. R. (2000). The effect of ultraviolet radiation on the vertical distribution and mortality of estuarine zooplankton. *Journal of Plankton Research* **22**, 2325–2350.

Spencer, M. & Blaustein, L. (2001a). Hatching responses of temporary pool invertebrates to signals of environmental quality. *Israel Journal of Zoology* **47**, 397–418.

Spencer, M. & Blaustein, L. (2001b). Risk of predation and hatching of resting eggs in the ostracod *Heterocypris incongruens*. *Journal of Crustacean Biology* **21**, 575–581.

Sprules, W. G. (1992). Non-video optical instruments for studying zooplankton distribution and abundance. *Archiv Für Hydrobiologie Ergebnisse der Limnologie* **36**, 45–58.

Sprules, W. G., Jin, E. H., Herman, A. W. & Stockwell, J. D. (1998). Calibration of an optical plankton counter for use in fresh water. *Limnology and Oceanography* **43**, 726–733.

Stanton, T. K. (2012). 30 years of advances in active bioacoustics: a personal perspective. *Methods in Oceanography* **1**, 49–77.

Stanton, T. K., Wiebe, P. H., Chu, D., Benfield, M. C., Scanlon, L., Martin, L. & Eastwood, R. L. (1994). On acoustic estimates of zooplankton biomass. *ICES Journal of Marine Science* **51**, 505–512.

Stich, H. B. & Lampert, W. (1984). Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. *Oecologia* **61**, 192–196.

Stoeckle, M. Y., Soboleva, L. & Charlop-Powers, Z. (2017). Aquatic environmental DNA detects seasonal fish abundance and habitat preference in an urban estuary. *PLoS One* **12**, e0175186.

Strachan, S. R., Chester, E. T. & Robson, B. J. (2015). Freshwater invertebrate life history strategies for surviving desiccation. *Springer Science Reviews* **3**, 57–75.

Strand, E., Bagøien, E., Edwards, M., Broms, C. & Klevjer, T. (2020). Spatial distributions and seasonality of four *Calanus* species in the Northeast Atlantic. *Progress in Oceanography* **185**, 102344.

Strand, E., Huse, G. & Giske, J. (2002). Artificial evolution of life history and behavior. *The American Naturalist* **159**, 624–644.

Straus-Dukerheim, M. (1815). Sur les *Daphnia*. *Mémoires du Muséum d'histoire Naturelle* **5**, 380–420.

Strickler, J. R. & Twombly, S. (1975). Reynolds number, diapause, and predatory copepods: with 2 figures and 1 table in the text. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* **19**, 2943–2950.

Strömberg, J.-O., Spicer, J., Liljebladh, B. & Thomasson, M. (2002). Northern krill, *Meganyctiphanes norvegica*, come up to see the last eclipse of the millennium? *Journal of the Marine Biological Association of the United Kingdom* **82**, 919–920.

Sullivan, B. K. (1980). In situ feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station "P". *Limnology and Oceanography* **25**, 317–326.

Svetlichny, L. S., Hubareva, E. S., Erkan, F. & Gucu, A. C. (2000). Physiological and behavioral aspects of *Calanus euxinus* females (Copepoda: Calanoida) during vertical migration across temperature and oxygen gradients. *Marine Biology* **137**, 963–971.

Swain, W. (1970). The ecology of the second trophic level in lakes superior, Michigan and Huron. *University of Minnesota Water Resources Center Bulletin* **26**, 1–151.

Swain, W. & Roijackers, K. (1985). Freshwater zooplankton sampling reconsidered: preliminary results of a high-speed sampling device for small lakes. *Hydrobiological Bulletin* **19**, 139–152.

Sweatt, A. J. & Forward, R. B. (1985a). Diel vertical migration and photoresponses of the chaetognath *Sagitta hispida* Conant. *The Biological Bulletin* **168**, 18–31.

Sweatt, A. J. & Forward, R. B. (1985b). Spectral sensitivity of the chaetognath *Sagitta hispida* Conant. *The Biological Bulletin* **168**, 32–38.

Sydeman, W. J. & Bograd, S. J. (2009). Marine ecosystems, climate and phenology: introduction. *Marine Ecology Progress Series* **393**, 185–188.

Taberlet, P., Coissac, E., Hajibabaei, M. & Rieseberg, L. H. (2012). Environmental DNA. *Molecular Ecology* **21**, 1789–1793.

Tarling, G., Jarvis, T., Emsley, S. & Matthews, J. (2002). Midnight sinking behaviour in *Calanus finmarchicus*: a response to satiation or krill predation? *Marine Ecology Progress Series* **240**, 183–194.

Tarling, G. A. (2003). Sex-dependent diel vertical migration in northern krill *Meganyctiphanes norvegica* and its consequences for population dynamics. *Marine Ecology Progress Series* **260**, 173–188.

Tarling, G. A., Buchholz, F. & Matthews, J. (1999). The effect of lunar eclipse on the vertical migration behaviour of *Meganyctiphanes norvegica* (Crustacea: Euphausiacea) in the Ligurian Sea. *Journal of Plankton Research* **21**, 1475–1488.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Tarling, G. A., Burrows, M., Matthews, J., Saborowski, R., Buchholz, F., Bedo, A. & Mayzaud, P. (2000). An optimisation model of the diel vertical migration of northern krill (*Meganyctiphanes norvegica*) in the Clyde Sea and the Kattegat. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 38–50.

Tarrant, A. M., Baumgartner, M. F., Verslycke, T. & Johnson, C. L. (2008). Differential gene expression in diapausing and active *Calanus finmarchicus* (Copepoda). *Marine Ecology Progress Series* **355**, 193–207.

Tattersall, W. M. (1911). Schizopodous Crustacea from the north-East Atlantic slope: second supplement. *Scientific Investigations of the Fisheries Research Board of Ireland* **2**, 1–77.

Terazaki, M. & Miller, C. B. (1986). Life history and vertical distribution of pelagic chaetognaths at Ocean Station P in the subarctic Pacific. *Deep Sea Research Part A. Oceanographic Research Papers* **33**, 323–337.

Teuber, L., Hagen, W., Bode, M. & Auel, H. (2019). Who is who in the tropical Atlantic? Functional traits, ecophysiological adaptations and life strategies in tropical calanoid copepods. *Progress in Oceanography* **171**, 128–135.

Thygesen, U. H. & Patterson, T. A. (2018). Oceanic diel vertical migrations arising from a predator-prey game. *Theoretical Ecology* **12**, 17–29.

Tiberti, R. & Iacobuzio, R. (2013). Does the fish presence influence the diurnal vertical distribution of zooplankton in high transparency lakes? *Hydrobiologia* **709**, 27–39.

Tilden, A. R., McCoole, M. D., Harmon, S. M., Baer, K. N. & Christie, A. E. (2011). Genomic identification of a putative circadian system in the cladoceran crustacean *Daphnia pulex*. *Comparative Biochemistry and Physiology Part D: Genomics and Proteomics* **6**, 282–309.

Timonin, A., Arashkevich, E., Drits, A. & Semenova, T. (1992). Zooplankton dynamics in the northern Benguela ecosystem, with special reference to the copepod *Calanoides carinatus*. *South African Journal of Marine Science* **12**, 545–560.

Tont, S. A. & Wick, G. L. (1973). Response of a deep scattering layer to the 1072 total solar eclipse. *Deep Sea Research and Oceanographic Abstracts* **20**, 769–771.

Torres, J., Aarset, A., Donnelly, J., Hopkins, T. L., Lancraft, T. & Ainley, D. (1994a). Metabolism of Antarctic micronektonic Crustacea as a function of depth of occurrence and season. *Marine Ecology Progress Series* **113**, 207–219.

Torres, J., Donnelly, J., Hopkins, T. L., Lancraft, T., Aarset, A. & Ainley, D. (1994b). Proximate composition and overwintering strategies of Antarctic micronektonic Crustacea. *Marine Ecology Progress Series* **5**, 221–232.

Tremblay, N., Gómez-Gutiérrez, J., Zenteno-Savín, T., Robinson, C. J. & Sánchez-Velascoa, L. (2010). Role of oxidative stress in seasonal and daily vertical migration of three krill species in the Gulf of California. *Limnology and Oceanography* **55**, 2570–2584.

Tsuda, A., Saito, H. & Kasai, H. (2004). Life histories of *Eucalanus bungii* and *Neocalanus cristatus* (Copepoda: Calanoida) in the western subarctic Pacific Ocean. *Fisheries Oceanography* **13**, 10–20.

Tsugeki, N. K., Ishida, S. & Urabe, J. (2009). Sedimentary records of reduction in resting egg production of *Daphnia galeata* in Lake Biwa during the 20th century: a possible effect of winter warming. *Journal of Paleolimnology* **42**, 155–165.

Urmy, S. S., Williamson, C. E., Leach, T. H., Schladow, S. G., Overholt, E. P. & Warren, J. D. (2016). Vertical redistribution of zooplankton in an oligotrophic lake associated with reduction in ultraviolet radiation by wildfire smoke. *Geophysical Research Letters* **43**, 3746–3753.

Ussing, H. H. (1938). *The Biology of Some Important Plankton Animals in the Fjords of East Greenland: Treaarsexpeditionen Til Christian den X's Land 1931–34*. Reitzel, Copenhagen.

Uye, S. (1980). Development of neritic copepods *Acartia clausi* and *A. steueri*. II. Isochronal larval development at various temperatures. *Bulletin of the Plankton Society of Japan* **27**, 11–18.

Uye, S. (1985). Resting egg production as a life history strategy of marine planktonic copepods. *Bulletin of Marine Science* **37**, 440–449.

Uye, S., Huang, C. & Onbe, T. (1990). Ontogenetic diel vertical migration of the planktonic copepod *Calanus sinicus* in the Inland Sea of Japan. *Marine Biology* **104**, 389–396.

van de Meutter, F., Stoks, R. & De Meester, L. (2008). Size-selective dispersal of *Daphnia* resting eggs by backswimmers (*Notonecta maculata*). *Biology Letters* **4**, 494–496.

van Ginneken, V. J. T. & Maes, G. E. (2005). The European eel (*Anguilla Anguilla*, Linnaeus), its lifecycle, evolution and reproduction: a literature review. *Reviews in Fish Biology and Fisheries* **15**, 367–398.

van Gool, E. & Ringelberg, J. (1998). Light-induced migration behaviour of *Daphnia* modified by food and predator kairomones. *Animal Behaviour* **56**, 741–747.

van Haren, H. & Compton, T. J. (2013). Diel vertical migration in Deep Sea plankton is finely tuned to latitudinal and seasonal day length. *PLoS One* **8**, e64435.

Vanschoenwinkel, B., Gielen, S., Seaman, M. & Brendonck, L. (2008). Any way the wind blows-frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* **117**, 125–134.

Varpe, Ø. (2012). Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. *Journal of Plankton Research* **34**, 267–276.

Varpe, Ø. & Ejsmond, M. J. (2018a). Semelparity and iteroparity. In *The Natural History of the Crustacea: Life Histories* (eds M. Thiel and G. Welborn), pp. 97–123. Oxford University Press, Oxford.

Varpe, Ø. & Ejsmond, M. J. (2018b). Trade-offs between storage and survival affect diapause timing in capital breeders. *Evolutionary Ecology* **32**, 623–641.

Varpe, Ø. & Fiksen, Ø. (2010). Seasonal plankton–fish interactions: light regime, prey phenology, and herring foraging. *Ecology* **91**, 311–318.

Varpe, Ø., Jørgensen, C., Tarling, G. A. & Fiksen, Ø. (2009). The adaptive value of energy storage and capital breeding in seasonal environments. *Oikos* **118**, 363–370.

Vegis, A. (1964). Dormancy in higher plants. *Annual Review of Plant Physiology* **15**, 185–224.

Verheye, H. M., Hutchings, L. & Peterson, W. (1991). Life history and population maintenance strategies of *Calanoides carinatus* (Copepoda: Calanoida) in the southern Benguela ecosystem. *South African Journal of Marine Science* **11**, 179–191.

Vinogradov, M., Arashkevich, E. & Ilchenko, S. (1992). The ecology of the *Calanus ponticus* population in the deeper layer of its concentration in the Black Sea. *Journal of Plankton Research* **14**, 447–458.

Visser, A. W., Grønning, J. & Jónasdóttir, S. H. (2017). *Calanus hyperboreus* and the lipid pump. *Limnology and Oceanography* **62**, 1155–1165.

Visser, A. W. & Jónasdóttir, S. H. (1999). Lipids, buoyancy and the seasonal vertical migration of *Calanus finmarchicus*. *Fisheries Oceanography* **8**, 100–106.

Vlymen, W. J. (1970). Energy expenditure of swimming copepods. *Limnology and Oceanography* **15**, 348–356.

Vogedes, D., Varpe, Ø., Søreide, J. E., Graeve, M., Berge, J. & Falk-Petersen, S. (2010). Lipid sac area as a proxy for individual lipid content of arctic calanoid copepods. *Journal of Plankton Research* **32**, 1471–1477.

von Elert, E. & Pohnert, G. (2000). Predator specificity of kairomones in diel vertical migration of *Daphnia*: a chemical approach. *Oikos* **88**, 119–128.

Voss, S. & Mumm, H. (1999). Where to stay by night and day: size-specific and seasonal differences in horizontal and vertical distribution of *Chaoborus flavicans* larvae. *Freshwater Biology* **42**, 201–213.

Wallace, M. I., Cottier, F. R., Berge, J., Tarling, G. A., Griffiths, C. & Brierley, A. S. (2010). Comparison of zooplankton vertical migration in an ice-free and a seasonally ice-covered Arctic fjord: an insight into the influence of sea ice cover on zooplankton behavior. *Limnology and Oceanography* **55**, 831–845.

Wallace, R., Gomez, H., Ayala, G. & Espinoza, F. (2003). Camera trapping for jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. *Mastozoología Neotropical* **10**, 133–139.

Walsh, M. R. (2013). The link between environmental variation and evolutionary shifts in dormancy in zooplankton. *Integrative and Comparative Biology* **53**, 713–722.

Wang, R., Zuo, T. & Wang, K. (2003). The Yellow Sea cold bottom water—an oversummering site for *Calanus sinicus* (Copepoda, Crustacea). *Journal of Plankton Research* **25**, 169–183.

Warren, J. D., Leach, T. H. & Williamson, C. E. (2016). Measuring the distribution, abundance, and biovolume of zooplankton in an oligotrophic freshwater lake with a 710 kHz scientific echosounder. *Limnology and Oceanography: Methods* **14**, 231–244.

Webster, C. N., Varpe, Ø., Falk-Petersen, S., Berge, J., Stübner, E. & Brierley, A. S. (2015). Moonlit swimming: vertical distributions of macrozooplankton and nekton during the polar night. *Polar Biology* **38**, 75–85.

Weider, L. J. & Lampert, W. (1985). Differential response of *Daphnia* genotypes to oxygen stress: respiration rates, hemoglobin content and low-oxygen tolerance. *Oecologia* **65**, 487–491.

Weikert, H. & John, H. (1981). Experiences with a modified Bé multiple opening-closing plankton net. *Journal of Plankton Research* **3**, 167–176.

Weismann, A. (1874). Ueber Bau-und Lebenserscheinungen von *Leptodora hyalina* Lilljeborg. In *Zeitschrift Fur Wissenschartliche Zoologie* (eds C. T. V. Siebold and A. V. Kölliker), pp. 349–448. Verlag von Wilhelm Engelmann, Leipzig.

Weismann, A. (1876). Zur Naturgeschichte der Daphnoiden. In *Wissenschaftliche Zoologie* (eds C. T. V. Siebold, A. V. Kölliker and E. Ehlers), pp. 51–112. W. Engelmann, Leipzig.

Wells, L. (1960). Seasonal abundance and vertical movements of planktonic crustacea in Lake Michigan. *Fishery Bulletin* **60**, 343–369.

Weng, K. C. & Block, B. A. (2004). Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital retia mirabilia. *Fishery Bulletin* **102**, 221–229.

Weng, K. C., Boustany, A. M., Pyle, P., Anderson, S. D., Brown, A. & Block, B. A. (2007). Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology* **152**, 877–894.

Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**, 1540–1548.

West, G. J. & Stevens, J. D. (2001). Archival tagging of school shark, *Galeorhinus galeus*, in Australia: initial results. In *The Behavior and Sensory Biology of Elasmobranch Fishes: An Anthology in Memory of Donald Richard Nelson* (eds T. C. Tricas and S. H. Gruber), pp. 283–298. Springer, Dordrecht.

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Whitmore, D., Foulkes, N. S. & Sassone-Corsi, P. (2000). Light acts directly on organs and cells in culture to set the vertebrate circadian clock. *Nature* **404**, 87–91.

Wiebe, P. H., Ashjian, C. J., Gallager, S. M., Davis, C. S., Lawson, G. L. & Copley, N. J. (2004). Using a high-powered strobe light to increase the catch of Antarctic krill. *Marine Biology* **144**, 493–502.

Wiebe, P. H. & Benfield, M. C. (2003). From the Hensen net toward four-dimensional biological oceanography. *Progress in Oceanography* **56**, 7–136.

Wiebe, P. H., Bucklin, A. & Benfield, M. C. (2017). Sampling, presercation and counting of samplers II: zooplankton. In *Marine Plankton: A Practical Guide to Ecology, Methodology, and Taxonomy* (eds C. Castellani and M. Edwards), pp. 104–139. Oxford University Press, Oxford.

Wiebe, P. H., Burt, K. H., Boyd, S. H. & Morton, A. W. (1976). A multiple opening/closing net and environmental sensing system for sampling zooplankton. *Journal of Marine Research* **34**, 313–326.

Wilcove, D. S. & Wikelski, M. (2008). Going, going, gone: is animal migration disappearing. *PLoS Biology* **6**, e188.

Williams-Howze, J. & Coull, B. C. (1992). Are temperature and photoperiod necessary cues for encystment in the marine benthic harpacticoid copepod *Heteropsyllus nunni* Coull? *The Biological Bulletin* **182**, 109–116.

Williamson, C. E., Fischer, J. M., Bollens, S. M., Overholt, E. P. & Breckenridge, J. K. (2011). Toward a more comprehensive theory of zooplankton diel vertical migration: integrating ultraviolet radiation and water transparency into the biotic paradigm. *Limnology and Oceanography* **56**, 1603–1623.

Williamson, C. E., Sanders, R. W., Moeller, R. E. & Paul, L. (1996). Utilization of subsurface food resources for zooplankton reproduction: implications for diel vertical migration theory. *Limnology and Oceanography* **41**, 224–233.

Williamson, D., Williamson, J. & Ngwamotsoko, K. T. (1988). Wildebeest migration in the Kalahari. *African Journal of Ecology* **26**, 269–280.

Wilson, R. J., Banas, N. S., Heath, M. R. & Speirs, D. C. (2016). Projected impacts of 21st century climate change on diapause in *Calanus finmarchicus*. *Global Change Biology* **22**, 3332–3340.

Wilson, R. J., Speirs, D. C. & Heath, M. R. (2013). Solid evidence or fluid ideas on the importance lipid phase transitions to diapausing copepods. *Journal of Plankton Research* **35**, 438–440.

Wilson, S. G., Polovina, J. J., Stewart, B. S. & Meekan, M. G. (2006). Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo reef, Western Australia. *Marine Biology* **148**, 1157–1166.

Winder, M., Boersma, M. & Spaak, P. (2003). On the cost of vertical migration: are feeding conditions really worse at greater depths? *Freshwater Biology* **48**, 383–393.

Winder, M. & Schindler, D. E. (2004). Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* **85**, 2100–2106.

Winder, M., Spaak, P. & Mooij, W. M. (2004). Trade-offs in *Daphnia* habitat selection. *Ecology* **85**, 2027–2036.

Winker, D. M., Vaughan, M. A., Omar, A., Hu, Y., Powell, K. A., Liu, Z., Hunt, W. H. & Young, S. A. (2009). Overview of the CALIPSO mission and CALIOP data processing algorithms. *Journal of Atmospheric and Oceanic Technology* **26**, 2310–2323.

Winn, H. E., Goodyear, J. D., Kenney, R. D. & Petricig, R. O. (1995). Dive patterns of tagged right whales in the great south channel. *Continental Shelf Research* **15**, 593–611.

Wirta, H. K., Vesterinen, E. J., Hambäck, P. A., Weingartner, E., Rasmussen, C., Reneerkens, J., Schmidt, N. M., Gilg, O. & Roslin, T. (2015). Exposing the structure of an Arctic food web. *Ecology and Evolution* **5**, 3842–3856.

Wissel, B. & Ramacharan, C. W. (2003). Plasticity of vertical distribution of crustacean zooplankton in lakes with varying levels of water colour. *Journal of Plankton Research* **25**, 1047–1057.

Wolcott, G. (1934). The diapause portion of the larval period of *Diaprepes abbreviatus* L. *Journal of Agriculture of the University of Puerto Rico* **18**, 417–427.

Wold, A. & Norrbin, F. (2004). Vertical migration as a response to UVR stress in *Calanus finmarchicus* females and nauplii. *Polar Research* **23**, 27–34.

Wood, T. R. (1932). Resting eggs that fail to rest. *The American Naturalist* **66**, 277–281.

Worthington, E. B. (1931). Vertical movements of fresh-water macroplankton. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **25**, 394–436.

Wroblewski, J. (1982). Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone—a simulation. *Deep Sea Research Part A. Oceanographic Research Papers* **29**, 665–686.

Yurista, P., Kelly, J. R. & Miller, S. (2005). Evaluation of optically acquired zooplankton size-spectrum data as a potential tool for assessment of condition in the Great Lakes. *Environmental Management* **35**, 34–44.

Zadereev, E. & Lopatina, T. (2007). The induction of diapause in *Moina* by species-specific chemical cues. *Aquatic Ecology* **41**, 255–261.

Zadereev, Y. S. (2003). Maternal effects, conspecific chemical cues, and switching from parthenogenesis to gametogenesis in the cladoceran *Moina macrocopa*. *Aquatic Ecology* **37**, 251–255.

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

Zeng, H., Qian, Z., Myers, M. P. & Rosbash, M. (1996). A light-entrainment mechanism for the *Drosophila* circadian clock. *Nature* **380**, 129–135.

Zhao, G., Ljungholm, M., Malmqvist, E., Bianco, G., Hansson, L.-A., Svanberg, S. & Brydegaard, M. (2016). Inelastic hyperspectral lidar for profiling aquatic ecosystems. *Laser & Photonics Reviews* **10**, 807–813.

Zhao, G., Malmqvist, E., Rydhmer, K., Strand, A., Bianco, G., Hansson, L.-A., Svanberg, S. & Brydegaard, M. (2018). Inelastic hyperspectral lidar for aquatic ecosystems monitoring and landscape plant scanning test. In *EPJ Web Conferences, No. 176*, pp. 1–4. EDP Sciences, Bucharest.

Zink, R. M. (2002). Towards a framework for understanding the evolution of avian migration. *Journal of Avian Biology* **33**, 433–436.

Zweerus, N. L., Sommer, S., Fontaneto, D. & Ozgul, A. (2017). Life-history responses to environmental change revealed by resurrected rotifers from a historically polluted lake. *Hydrobiologia* **796**, 121–130.

(*Received 2 January 2020; revised 18 March 2021; accepted 19 March 2021; published online 4 May 2021*)

1469185x, 2021, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.12715 by Bibliothèque de Sorbonne Université, Wiley Online Library on [24/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License