ORIGINAL ARTICLE

Sleep walking copepods? *Calanus* diapausing in hypoxic waters adjust their vertical position during winter

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While hypoxia is generally associated with negative connotations, some animals may also take advantage of reduced oxygen concentrations. However, the dynamics of such processes for zooplankton are poorly understood. We made continuous acoustic studies of *Calanus helgolandicus* overwintering in hypoxic waters (Oslofjorden, Norway). Their apparent minimum oxygen tolerance was 0.2–0.3 mL O2 L−1 at 8°C. The copepods adjusted their vertical distribution in concert with the upward progression of hypoxia as oxygen contents declined in the course of winter. The hypoxic overwintering habitat largely excluded potential predators and mortality appeared low in early winter. As the copepod distribution shallowed in phase with declining oxygen contents at depth, mortality increased. In contrast to recent predictions, *C. helgolandicus* had sufficient energy reserves to sustain long-term overwintering. Termination of the overwintering phase in spring was gradual but appeared to accelerate during the development of the spring bloom. Enhanced oceanic deoxygenation with climate change may affect seasonally migrating copepods in unpredictable ways.

KEYWORDS: *Calanus helgolandicus*; overwintering; dormancy; ocean deoxygenation
INTRODUCTION

Climate change affects pelagic ecosystems through various mechanisms. For example, higher temperatures cause poleward movements of biogeographic boundaries, also for numerous copepod species (Reygondeau and Beaufort, 2017; Chivers et al., 2019). Oxygen concentrations in the open ocean and coastal waters are declining, and both coastal hypoxia and oceanic deoxygenation are predicted to worsen with increasing global temperatures (Levin and Breitburg, 2015; Breitburg et al., 2018). Ocean deoxygenation may cause both losers and winners among plankton (Wishner et al., 2015). Some may be excluded from previous habitats, while others may exploit low oxygen waters. Wishner et al. (2020) termed organisms being specially adapted to live in oxygen minimum zones for “hypoxiphilic.” Yet, many others may tolerate low oxygen and take advantage of hypoxic habitats on different time scales, e.g. for predator avoidance during either a daily cycle or during diapause (Nolan et al., 2019; Wishner et al., 2020).

The life cycle of temperate and high latitude copepods often includes a dormant overwintering phase in deep waters. Understanding the dormant life-phase of calanoid copepods has long been an aim of biological oceanography (Pond, 2012). Calanus spp. are key copepods in the Northern Atlantic (Conover, 1988). Generally, research has centered on C. finmarchicus, but the ongoing northward distribution shift of the congener C. helgolandicus in response to warming (Fromentin and Planque, 1996; Beaugrand et al., 2003), warrants more focus on the less studied C. helgolandicus (Bonnet et al., 2005).

The dormancy phase of Calanus spp. varies among species and regions (Conover, 1988; Krile et al., 2019) and is less understood for C. helgolandicus than for its northern congeneric (Bonnet et al., 2005; Wilson et al., 2015). In some habitats, C. helgolandicus seems active in upper waters throughout winter (Conover, 1988), while populations in other locations may overwinter in diapause (Hallberg and Hirche, 1980; Hirche, 1983, 1984). Wilson et al., (2015) argued that energy reserves of C. helgolandicus would sustain diapause for < 60 days in most of its geographic range, where temperatures exceed 10°C. They reasoned that the potential inability to diapause for longer periods might largely restrict C. helgolandicus to continental shelf regions (Wilson et al., 2015).

Calanus helgolandicus is the prevailing Calanus-species in the Oslofjord, as established with both morphological and molecular methods (Beyer et al., 1967; Bagoien et al., 2000; Bucklin et al., 1999). The deepwater of the inner fjord often becomes hypoxic. Bagoien et al. (2000) studied the seasonal migration of Calanus spp. in the fjord but did not sample in the inner, hypoxic part. We are unaware of studies addressing the tolerance of C. helgolandicus to hypoxia. However, Calanus euxinus in the Black Sea enters diapause and aggregates near the lower boundary of the oxygen zone (Vinogradov et al., 1992; Sakinan and Gücçü, 2017). This species is closely related to—and originally was classified as—C. helgolandicus (Unal et al., 2006). Similarly, Osgood and Checkley (1997a, b) found high concentrations of resting Calanus pacificus just above oxygen deficient bottom waters in Santa Barbara Basin. There, the copepods adjusted their distribution upwards so oxygen concentrations declined, but still inhabited waters with very low oxygen levels (Osgood and Checkley, 1997a, b).

We made continuous acoustic measurements for ~4 months of C. helgolandicus overwintering in hypoxic waters of the inner Oslofjord. The acoustic target identity was confirmed with intermittent net sampling during the study period. The acoustic observations documented apparent patterns in mortality, adjustments of vertical distribution reflecting limits of tolerance to hypoxia, as well as duration of the overwintering phase. The acoustic data moreover unveiled small-scale vertical patchiness of the overwintering population in the enclosed basin water below sill depth. While the study presents novel data with an unsurpassed temporal and vertical resolution on this particular Calanus species, it more generally represents a model of a diapausing copepod population responding to a changing physical and biological environment during the course of dormancy.

METHODS

Study site

We studied overwintering C. helgolandicus in the 150 m deep Bunnefjorden, the inner branch of the Oslofjord (59.792171°N, 10.726776°E; Fig. 1 in Klevjer and Kaartvedt, 2011). This is a very sheltered location separated from the outer parts of the fjord by a 57 m deep sill. The residence time of the deep waters is about 3–4 years (Gade, 1973) and waters below the sill commonly become hypoxic (Solberg et al., 2015).

Acoustics

We made acoustic measurements at 200 kHz for 4 months during winter and spring 2007–2008, supplemented by intermittent field campaigns. The virtual absence of other macrofauna in the low oxygen water (e.g. Solberg and Kaartvedt, 2017) facilitated the acoustic target identification and enabled the use of instrument settings that made the echosounder sufficiently sensitive to record the
Field campaigns

We conducted field campaigns in December 2007 and in January, February and April 2008. Vertical profiles of temperature and salinity were measured by CTD (Conductivity, Temperature and Depth) equipped with Niskin bottles. Water samples from 13 depths between the surface and 150 m (bottom) were analyzed for oxygen content using the standard Winkler method (except for April). Vertical profiles of temperature, salinity and oxygen from the entire water column are given in Solberg and Kaartvedt (2017; their Fig. 2). We therefore here only provide data on density and oxygen below 60 m.

Daytime vertical net tows for mesozooplankton (except for January) were made over six depth intervals (bottom–100 m, 100–80 m, 80–60 m, 60–40 m, 40–20 m, 20–0 m) using a WP-2 net. Species identification of Calanus was made based on microscopically checking the coxopodite curvature of the fifth pair of swimming legs (cf. Sars, 1903; Fleming and Hulsemann, 1977) on 20 individuals in samples from the bottom to 100 m (December), 100–80 (February) and 80–60 (April). Only C. helgolandicus occurred in these subsamples (mostly stage CV). We, therefore, assigned Calanus sp. in the remaining samples to C. helgolandicus.

RESULTS

Diel echogram at threshold –80 dB

A diel echogram (February) illustrates how hypoxic waters (see below) excluded much of the macrofauna (Fig. 1). Echoes of vertically migrating krill and fish prevailed in the upper 60 m. There was a sharp boundary toward waters below, which were largely devoid of backscatter at a –80 dB threshold, apart from some weak backscatter at ~80–100 m (Fig. 1). There was no diel pattern in the hypoxic waters.

Hydrography, net tows and low-threshold acoustic (–90 dB)

The temperature was about 8°C and salinity 33 in the deeper part of the water column all winter, with only slight changes with depth in the basin water (data presented in Solberg and Kaartvedt, 2017). The density increased slightly toward the bottom, most sharply above about 80 m. Profiles were very similar throughout the study period, though bottom waters appeared slightly less dense at the end of the study (Fig. 2). Oxygen concentrations were < 0.8 mL O₂ L⁻¹ below 60 m and declined both with depth and time (Fig. 2). Oxygen concentrations...
in waters just above the bottom were about 0.3 mL O₂ L⁻¹ in December and 0.1 mL O₂ L⁻¹ in February. At 130 m concentrations declined from 0.4 to 0.2 mL O₂ L⁻¹ in the course of that period and a corresponding declining trend occurred throughout the basin water.

*C. helgolandicus* CV made up nearly 90% in terms of numbers of the zooplankton captured in the hypoxic waters below 60 m, with the small copepods *Oithona* and *Oncea* dominating the remainder. In December and early winter, abundances were high in deeper parts of the water column with an average of ~500 individuals m⁻³ in the 50 m depth interval from 100 m to the bottom. Abundance declined with shoaling depth (Fig. 2).

In February, the copepods stayed shallower, with peak concentrations of ~800 copepods m⁻³ at 100–80 m, while concentrations below had decreased markedly. The integrated abundance of *Calanus* in net catches declined from 31 540 individuals m⁻³ in December to 23 050 individuals m⁻³ in mid-February. In April, the copepods had virtually disappeared below 80 m. Stage CVI females now constituted about 50% of the *Calanus*-population and dominated in catches above 60 m (not shown).

The low-threshold acoustic records of the weak targets in the hypoxic waters agreed well with the distribution of *Calanus* in the net samples (Fig. 2). The higher vertical resolution in the acoustic data (averages for whole months) indicates that the majority of *Calanus* captured at 130–100 m in December stems from the lower half of this depth interval. In February, the weak acoustic record in the deepest part of the water column and the marked acoustic maximum at 80–90 m mirrored the distribution of *Calanus* in the net catches. In April, neither catches nor acoustic records documented much *Calanus* below 80 m. There then was a slight discrepancy with somewhat deeper acoustic records compared with the net tows. The acoustic data were averaged for the April records, while the net tows were taken at the end of the study period (Fig. 2).
Continuous long-term acoustics records in hypoxic waters

At the start of winter, backscatter below the strong echoes of krill and fish in the in the more oxygenated part of the water column increased with depth, apart for a narrow zone just above the bottom, which was devoid of backscatter (Fig. 3). From mid-January, a band of stronger echoes appeared at ∼90 m. This band developed into a progressively stronger maximum in February and had disappeared by mid-March. Parallel to the strengthening of this thin layer, echoes became weaker below, until virtually disappearing at ∼10 February. Waters below
80 m were devoid of backscatter toward the end of the registration period.

Abundance, as proxied by integrated backscatter (NASC) in the hypoxic waters, initially remained stable with time. There was a sudden decline from early February, with an apparent subsequent accelerated decline from early/mid-March (Fig. 3).

**Patchiness/vertical stratification**

Resolving the deep acoustic data on a diel scale revealed repeated dense layers alternating with depth intervals without backscatter in the hypoxic water (Fig. 4). The vertical positions of the thin acoustic layers varied somewhat on short-time scales, but not always in synchrony (Fig. 4).

**DISCUSSION**

We have presented results on seasonally migrating copepods, applying an echosounder cabled to shore providing data of supreme temporal and vertical resolution. As the backscatter followed a seasonal development similar to that of *C. helgolandicus* in net samples and because there were no alternative acoustic targets in the hypoxic waters, we used the continuous long-termed acoustic records to assess the abundance and vertical distribution throughout winter.

While *Calanus finmarchicus* generally diapause, *C. helgolandicus* appears more variable (Bonnet *et al.*, 2005). The *Calanus* overwintering strategy depends on lipid energy storage. Wilson *et al.* (2015) argued that the period of dormancy would be less than 60 days in *C. helgolandicus* at temperatures comparable to those in our study. However, our direct observations revealed a much longer overwintering period. In Oslofjorden *C. helgolandicus* initiates overwintering and descends during September (Bagøien *et al.*, 2000). Regardless of any inter-annual variations, the overwintering population was well established at depth when we initiated acoustic sampling in early December. An accelerated decline in the acoustic backscatter ascribed to *Calanus* during March (cf. Fig. 3) was likely influenced by the initiation of the seasonal ascent associated with the termination of overwintering. This timing matched with the development of the spring bloom (Røstad and Kaartvedt, 2013). While most individuals had terminated overwintering by April, some *C. helgolandicus* remained at depth after the bloom. Similar, and probably state-dependent, long stretched periods of diapause termination over several months occur in other, better oxygenated parts of Oslofjorden (Bagøien *et al.*, 2000).
Hypoxia tolerant zooplankton living near their physiological limits may respond to very slight changes in oxygen (Wishner et al., 2018). As oxygen concentrations declined at depth during winter, the overwintering C. helgolandicus adjusted their vertical distribution upwards (Figs 2 and 3). From the vertical relocation relative to the ambient oxygen concentrations, we derive that their lower tolerance is between 0.2 and 0.3 mL O₂ L⁻¹ at 8°C. Such values compare well with those at which *Calanus pacificus* may diapause, also occurring in waters of 0.2–0.3 mL O₂ L⁻¹ (Alldredge et al., 1984; Osgood and Checkley, 1997a, b). Also in other settings, zooplankton abundance and biomass appear to decrease sharply when oxygen levels fall below 0.2 mL O₂ L⁻¹ (Longhurst, 1967; Böttger-Schnack, 1996; Ekau et al., 2010). There was no change in water density explaining the shallowing distribution. The enclosed basin water was resident throughout winter as evidenced by the continuous decline in oxygen contents and without signs of intrusion of denser waters. However, we cannot exclude the passive upward movement of animals with differences in lipid composition.

Lipids aid in buoyancy (Pond, 2012), become sequestrated during winter (Jónasdóttir et al., 2019), yet overwintering copepods may be slightly positive buoyant (Visser and Jónasdóttir, 1999).

By overwintering in hypoxic waters, the copepods were partly, but not totally protected from predators. The net samples from 13 December and 12 February suggest some (~30%) reduction in surface integrated abundance in the course of that 2 month period. While the nets only represent two sampling dates without replicates, the integrated backscatter ascribed to *Calanus* provides a continuous picture. Backscatter remained stable until suddenly higher rates of decline appeared from mid-February, concurring with the formation of a dense copepod layer at 80–100 m (Figs 2 and 3).

Some invertebrate predators like chaetognaths can tolerate low oxygen values and may co-occur with copepods in low oxygen waters (Sakinan and Gucii, 2017), but none were captured below 100 m during the current study (Røstad and Kaartvedt, 2013). In this fjord branch fish and krill generally avoid the lower part of the water.
column when oxygen deficit (e.g. Fig. 1; Kaartvedt et al., 2009; Solberg et al., 2015). However, planktivorous fish (sprat; Sprattus sprattus) made occasional short excursions into the low oxygen water, apparently foraging on the overwintering Calanus during this winter (Solberg and Kaartvedt, 2017). In early winter the bulk of Calanus inhabited near-bottom waters (Fig. 2) and was out of reach for such short-range and short-time forays, but sprat dived into the shallowing Calanus-layer later in winter (Solberg and Kaartvedt, 2017). Calanus would become more accessible to the planktivorous fish when moving upwards and concentrating closer to the oxycline that defines the lower depth of the main sprat distribution. Calanus indeed dominated the prey in sprat stomachs this particular winter (Solberg and Kaartvedt, 2017). While we cannot exclude other causes of mortality (cf. Daase et al., 2014) predation appears to be the most plausible explanation for the enhanced decline in Calanus numbers in mid-winter when vertical distribution became progressively shallower. Advection is an unlikely explanation for the observed population decline, as the water properties attested to an enclosed water mass below the sill depth of Bunefjorden throughout the study.

Similarly to our interpretation, studies elsewhere have shown that hypoxia can lead to a decoupling of predator–prey interactions (Taylor and Rand, 2003), with the spatial extent of the suitable habitat for fish declining during hypoxic events, while zooplankton may find refuge from predation. Thus, hypoxic conditions may reduce the predation risk of zooplankton from pelagic fish (Taylor and Rand, 2003), although examples of fish exploiting high zooplankton concentrations in hypoxic waters also exist. For example, anchovy may make short-range/term excursions into hypoxic waters with concentrated zooplankton prey (Taylor et al., 2007). Alternatively, if enhanced hypoxia would force the copepods even further upwards, low oxygen might instead be detrimental by making the copepods more vulnerable to visual predators, as suggested for other predator/prey relations with expanding oxygen minimum zones (e.g. Netburn and Koslow, 2015). In this way, hypoxia-related to coastal eutrophication and climate change may alter trophic fluxes through food webs in non-linear ways. The effects of long-term climate-driven changes remain hard to predict, also because marine food webs are more complex than simply considering the spatial overlap between plankton and fish as focused on here (Ekau et al., 2010).

The backscatter ascribed to overwintering Calanus displayed a strikingly stratified vertical structure. We have not resolved the role of passive versus active accumulation. Pond (2012) argued that achieving neutral buoyancy is essential for copepods that overwinter in diapause since active swimming will both attract predators, and deplete metabolic energy reserves. Zooplankton may accumulate passively in response to density gradients in the environment (Tiselius et al., 1994). Some slight apparent vertical variations on short-time scales (Fig. 4) probably reflected physical displacements of the water rather than individuals actively relocating. However, layers and aggregations may also form actively in response to chemical (e.g. Heuschele and Selander, 2014) or physical conditions, invoked both directly by the environment per se (Buskey et al., 1995) or indirectly via for example cues emitted from predators or conspecifics (Heuschele and Selander, 2014; Leising and Yen, 1997). Copepods have a whole suite of sensory abilities and can detect and process at least chemical, hydrodynamic and light signals and alter their behavior and distribution in response, so sensory and behavioral mechanisms for maintaining such layers are in place.

CONCLUSION

C. helgolandicus in the Oslofjord sustained long-term overwintering in hypoxic waters. Their apparent minimum oxygen tolerance was 0.2–0.3 mL O2 L−1 at 8°C. The copepods adjusted their vertical distribution in concert with the upward progression of hypoxia as oxygen contents declined in the course of winter. Such apparent active shifts in vertical distribution during diapause have implications not only for our understanding of altered distribution patterns in response to future climate scenarios but also for predictions of population mortality during winter.

DATA ARCHIVING

Data are available from the corresponding author upon request.

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REFERENCES

Alldredge, A. L., Robison, B. H., Fleminger, A., Torres, J. J., King, J. M. and Hamner, W. M. (1984) Direct sampling and in situ observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. Mar. Biol., 80, 75–81.
Bagenis, E., Kaartvedt, S. and Øveraas, S. (2000) Seasonal vertical migration of Calanus spp. in Oslofjorden. Sarsia, 85, 299–311.

Beaugrand, G., Branch, K. M., Lindley, J. A., Souissi, S. and Reid, P. C. (2003) Plankton effect on cod recruitment in the North Sea. Nature, 426, 661–664.

Beyer, F., Dylbwald, A. and Vervik, J. (1967) Oslofjorden og dens forurensningsproblemer. Zooplankton. I. Undersøkelsen 1962–1965. Delrapport nr. 5. Zooplankton, Norwegian Institute of Water Research, Oslo, p. 91.

Böttger-Schnack, R. (1996) Vertical structure of small metazoan plankton, especially non-calanoid copepods. I. Deep Arabian Sea. J. Plankton Res., 18, 1073–1101.

Bonnet, D., Richardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., Géballe, G., Diekmann, R. et al. (2005) An overview of Calanus helgolandicus ecology in European waters. Prog. Oceanogr., 65, 1–33.

Brecke, D., Levin, L. A., Oschlies, A., Godfrey, M. F., Chavez, P., Conley, D. J., Garcon, V., Gillett, D. et al. (2018) Declining oxygen in the global ocean and coastal waters. Science, 359, eaam7240.

Bucklin, A., Guarnieri, M., Hill, R. S., Bentley, A. and Kaartvedt, S. (1996) Taxonomic and systematic assessment of planktonic copepods using mitochondrial COI sequence variation and competitive, species-specific PCR. Hydrobiologia, 401, 239–254.

Buskey, E. J., Peterson, J. O. and Ambler, J. W. (1995) The role of photoreception in the swimming behavior of the copepod Diodonidae oculata. Mar. Freshw. Behav. Physiol., 26, 273–285.

Chivers, W. J., Walne, A. W. and Hays, G. C. (2017) Mismatch between marine plankton range movements and the velocity of climate change. Nat. Commun., 8, 14434.

Conover, R. J. (1988) Comparative life history in the genera Calanus and Nocalanus in high latitudes of the northern hemisphere. Hydrobiologia, 167/168, 127–142.

Daase, M., Varpe, O. and Falk-Petersen, S. (2014) Non-consumptive mortality in copepods: occurrence of Calanus spp. carcasses in the Arctic Ocean during winter. J. Plankton Res., 36, 129–144.

De Leo, F. C., Ogata, B., Sasri, A. R., Heesemann, M., Mihaly, D., Galbraith, M. and Morley, M. G. (2018) High-frequency observations from a deep-sea cabled observatory reveal seasonal overwintering of Neocalanus spp. in Barkley canyon, NE Pacific: insights into particulate organic carbon flux. Prog. Oceanogr., 169, 120–137.

Ekau, W., Axel, H., Portner, H. O. and Gilbert, D. (2010) Impacts of hypoxia on the structure and processes in the pelagic community (zooplankton, macro-invertebrates and fish). Biosciences, 7, 1669–1699.

Fleminger, A. and Hubemann, K. (1977) Geographical range and taxonomic divergence in North Atlantic Calanus (C. helgolandicus, C. finmarchicus and C. glacialis). Mar. Biol., 40, 233–248.

Fromentin, J.-M. and Planque, B. (1996) Calanus and environment in the eastern North Atlantic. II. Influence of the North Atlantic oscillation on C. finmarchicus and C. helgolandicus. Mar. Ecol. Prog. Ser., 134, 111–118.

Gade, H. G. (1973) Deep water exchanges in a sill fjord: a stochastic process. J. Phys. Oceanogr., 3, 213–219.

Hallberg, E. and Hirsche, H.-J. (1980) Differentiation of mid-gut in adults and over-wintering copepods of Calanus finmarchicus (Gunnerus) and C. helgolandicus Claus. J. Exp. Mar. Biol. Ecol., 48, 283–293.

Heuschele, J. and Solander, E. (2014) The chemical ecology of copepods. J. Plankton Res., 36, 895–913.

Hirsche, H.-J. (1983) Overwintering of Calanus finmarchicus and Calanus helgolandicus. Mar. Ecol. Prog. Ser., 11, 201–290.

Hirsche, H.-J. (1984) Seasonal distribution of Calanus finmarchicus (Gunnerus) and C. helgolandicus (Claus) in a Swedish fjord. Crustaceana Supplement, 7, 233–241.

Jonassdottir, S. H., Wilson, R. J., Gislason, A. and Heath, M.-R. (2019) Lipid content in overwintering Calanus finmarchicus across the eastern subpolar North Atlantic Ocean. Limnol. Oceanogr., 64, 229–243.

Kaartvedt, S., Rostad, A. and Kleijer, T. A. (2009) Small euphausid fishes (Sprattus sprattus) can exploit low oxygen waters for overwintering. Mar. Ecol. Prog. Ser., 390, 237–249.

Kleijer, T. A. and Kaartvedt, S. (2011) Krill (Meganyctiphanes norvegica) swim faster at night. Limnol. Oceanogr., 56, 765–774.

Kvile, K. O., Ashjian, C. and Ji, R. (2019) Pan-Arctic depth distribution of Diapausing Calanus copepods. Biol. Bull., 237, 76–89.

Leising, A. W. and Yen, J. (1997) Spacing mechanisms within light-induced copepod swarms. Mar. Ecol. Prog. Ser., 155, 27–35.

Levin, L. A. and Breitburg, D. L. (2015) Linking coasts and seas to address ocean deoxygenation. Nature Climate Change, 5, 401–403.

Longhurst, A. R. (1967) Vertical distribution of zooplankton in relation to the eastern Pacific oxygen minimum. Deep-Sea Res., 14, 51–63.

Muth, E. (2003) Acoustical identification of the concentration layer of a copepod species, Calanus euxinus. Mar. Biol., 142, S17–S23.

Netburn, A. N. and Koslow, A. J. (2015) Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. Deep-Sea Res. I, 104, 149–158.

Nolan, S., Boltens, S. M. and Rollwagen-Bollens, G. (2019) Diverse taxa of zooplankton inhabit hypoxic waters during both day and night in a temperate eutrophic lake. J. Plankton Res., 41, 431–447.

Osgood, K. E. and Checkley, D. M. Jr. (1997a) Seasonal variations in a deep aggregation of Calanus pacificus in the Santa Barbara Basin. Mar. Ecol.-Prog. Ser., 148, 59–69.

Osgood, K. E. and Checkley, D. M. Jr. (1997b) Observations of a deep aggregation of Calanus pacificus in the Santa Barbara Basin. Limnol. Oceanogr., 42, 997–1001.

Pond, D. (2012) The physical properties of lipids and their role in controlling the distribution of zooplankton in the oceans. J. Plankton Res., 34, 443–453.

Reygondeau, G. and Beaugrand, G. (2011) Future climate-driven shifts in distribution of Calanus finmarchicus. Glob. Chang. Biol., 17, 756–766.

Rostad, A. and Kaartvedt, S. (2013) Seasonal and diet patterns in sedimentary flux of krill fecal pellets recorded by an echosounder. Limnol. Oceanogr., 58, 1985–1997.

Saknan, S. and Gucci, A. C. (2017) Spatial distribution of the Black Sea copepod, Calanus euxinus, estimated using multifrequency acoustic backscatter. ICES J. Mar. Sci., 74, 832–846.

Sars, G. O. (1903) An Account of the Crustaceans of Norway. IV Copepoda Calanoidea, Bergens Museum, Bergen, p. 171 108 pl.

Sollberg, I., Rostad, A. and Kaartvedt, S. (2015) Ecology of overwintering sprat (Sprattus sprattus). Prog. Oceanogr., 138, 116–135.

Sollberg, I. and Kaartvedt, S. (2017) The diet vertical migration patterns and individual swimming behavior of overwintering sprat (Sprattus sprattus). Prog. Oceanogr., 151, 49–61.

Staby, A., Rostad, A. and Kaartvedt, S. (2011) A full year study of diet vertical migration of the mesopelagic fish Maurolicus muelleri reveals novel and varied migration patterns. Mar. Ecol. Prog. Ser., 441, 241–255.

Taylor, J. C. and Rand, P. S. (2003) Spatial overlap and distribution of anchovies (Engraulis spp.) and copepods in a shallow stratified estuary. Aquat. Living Resour., 16, 191–196.
Taylor, J. C., Rand, P. S. and Jenkins, J. (2007) Swimming behavior of juvenile anchovies (Anchoa spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. *Mar. Biol.*, **152**, 939–957.

Tiselius, P., Nielsen, G. and Nielsen, T. G. (1994) Microscale patchiness of plankton within a sharp pycnocline. *J. Plankton Res.*, **16**, 543–554.

Unal, E., Frost, B. W., Armbrust, V. and Kimley, A. E. (2006) Phylogeography of *Calanus helgolandicus* and the Black Sea copepod *Calanus euxinus*, with notes on *Pseudocalanus elongatus* (Copepoda, Calanoida). *Deep-Sea Res. II*, **53**, 1961–1975.

Vinogradov, M. E., Arashkevich, E. G. and Ilchenko, S. V. (1992) The ecology of the *Calanus Ponticus* population in the deeper layer of its concentration in the Black-Sea. *J. Plankton Res.*, **14**, 447–458.

Wilson, R. J., Speirs, D. C. and Heath, M. R. (2015) On the surprising lack of differences between two congeneric calanoid copepod species, *Calanus finmarchicus* and *C. helgolandicus*. *Prog. Oceanogr.*, **134**, 413–431.

Wishner, K. F., Seibel, B., Roman, C., Deutsch, C., Outram, D., Shaw, C., Birk, M., Mislan, K. et al. (2018) Ocean deoxygenation and zooplankton; very small oxygen differences matter. *Sci. Adv.*, **4**, eaau5180. doi: 10.1126/sciadv.aau5180.

Wishner, K. F., Seibel, B. and Outram, D. (2020) Ocean deoxygenation and copepods: coping with oxygen minimum zone variability. *Biogeosciences*, **17**, 2315–2339.

Visser, A. W. and Jonsdottir, S. H. (1999) Lipids, buoyancy and the seasonal vertical migration of *Calanus finmarchicus*. *Fish. Oceanogr.*, **8**, 100–106.