

## COMMENT

**When lights are low: Comment on 'Midnight sinking behaviour in *Calanus finmarchicus*: a response to satiation or krill predation?' by Tarling et al. (2002)**

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It is very welcome to see Tarling et al.'s (2002) examination of the proximal causes ('cues') for diel vertical migration (DVM) in nature. New technologies such as the ADCP (acoustic Doppler current profiler) are certain to facilitate research into the bases of this vital phenomenon. However, I feel that there are omissions and some possible interpretation problems in this study.

One omission is of stratified samples of *Calanus* at different times during the day and night. Simple 'day' and 'night' samples are insufficient for tracking the movements of animals (Pearre 2000) and providing ground truthing for the ADCP data. Perhaps the most obvious and serious omission is of the examination of gut contents, without which it is very difficult to establish—or refute—satiation-cued descent in the water column (Pearre 2000; and see discussion in Pearre 2003). However, the degree of synchrony of the migrations can provide indirect information. For example, light signals affect whole populations simultaneously, and so should result in synchronous migrations. It is agreed that the response to a massed arrival of predators, such as Tarling et al. (2002) posit, might also result in a synchronous descent of the prey. By its nature however, satiation-based descent is usually asynchronous, especially in a patchy environment, as each animal is stimulated to descend individually as soon as it has sufficiently fed. Satiation-cued descent might cause midnight sinking, but it would generally only be observed as a vertical dispersal and a gradual increase of the mean depth of the population. Thus, even were satiation-cued descent also occurring, if the authors did find a synchronous descent event, they are probably correct that it was not caused by satiation.

Tarling et al.'s (2002) principal evidence for a synchronous descent of *Calanus* in this study is the large downward velocity signal found usually within an hour of the arrival of the predatory krill (especially *Mega-*

*nyctiphanes norvegica*) in the surface waters. The authors reported (p. 192) that, at the times and depths near the downward velocity anomaly, *Calanus* outnumbered krill in net samples by 25:1. Assuming that the *Calanus* population was not migrating, they calculated that there were too few krill to alone cause the large velocity anomaly at any reasonable migration speed. However, there seems no reason to assume that it must be one or the other: satiated krill and copepods could have been descending together. Numerous studies, including Tarling et al. (1999, 2001) have documented midnight sinking in *M. norvegica*, and several others have indicated individual movements out of the surface layer starting early in the evening, superimposed on normal DVMs (Simard et al. 1986, Buchholz et al. 1995, Onsrud & Kaartvedt 1998, Lass et al. 2001: see discussion in Pearre 2003: p. 28–29). If krill were also descending, their contribution would reinforce the signal and this would mean that the descent of *Calanus* need not have been so intense and synchronous.

One of the major challenges to the authors' thesis is posed by the data of Fig. 11 (late-stage *Calanus* and krill concentrations in the 0–20 m layer between 10:00 and 02:00 h in August). This appears to show that *Calanus* began leaving the surface in large numbers 2 h before the arrival of krill, so that, at least for August, the case for cueing of any massed *Calanus* descent by the krill seems difficult to make. However, allowing for the time shift, the ADCP data for August looked very similar to those for June and July (Figs. 4 & 5). It is regrettable that surface abundance data of similar type to those of Fig. 11 were not available for the other 2 months.

Referring especially to night samples of Stage V and adult females, the authors note (p. 191) that, in July, '... there were still a significant number of individuals present at almost all other [than surface] depths...'. In August, they note that 'Stage V differed from the other

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stages by the fact that individuals were also found in relatively large numbers in the deep (100 to 130 m) during the night.' In each case, why were the copepods deep (presumably not feeding) during the night? Rey-Rassat et al. (2002) have recently demonstrated that female *Calanus finmarchicus* that are manufacturing reproductive products require considerable extra energy and, as surmised by Manteyfel (1958), may be forced to spend more time feeding in the dangerous surface waters than they otherwise would have. This implies, by contrast, that a substantial proportion of the late-stage July animals and the August Stage V either failed to go to the surface or descended very early because they were nutritionally sufficed, rather than having differing need for, or means of, detecting predators. Several studies indicate that when food is scarce, herbivores may remain in the surface waters even under high threat of predation (e.g. Flik & Ringelberg 1993).

The authors cite 3 studies which, though having been used to support satiation-induced migration, they feel may instead be examples of predator-mediated midnight sinking. However, as Gauld (1953) could not detect synchronous migration at any time (no mass transfer), his study cannot be included as a case of midnight sinking: in that case neither light, nor predators, nor endogenous rhythm appears to have cued the up- or down-swimming. Midnight sinking was reported in the other 2 studies: Durbin et al. (1995) reported that, at one station, *Calanus finmarchicus* containing food were found in deep water early in the night, apparently indicating rapid downward movement of satiated animals, and corresponding to a small Stage IV/Stage V sinking event. However, the majority performed a unimodal DVM, remaining near the surface through most of the night. This does not seem to have the character of a large-scale, predator-cued migration. Simard et al. (1985) reported that although *Calanus* left the surface and stopped feeding during the night, many returned to the surface to feed again before dawn, presumably also to face the same suite of predators. Unfortunately, the August sampling schedule in the present study precluded obtaining data from the latter part of the night (02:00 to 10:00 h; see Fig. 11), which could have indicated if there was also a 'dawn rise' in this population.

The authors also state (p. 193) that the declining duration apparently spent in near-surface (feeding) locations through the season did not correspond to a seasonal increase in food abundance, as it should according to the hunger-satiation hypothesis. However, (1) the mean chl *a* concentration increased greatly from June to July ( $\times 6.3$ ), and declined only slightly in August ( $\times 0.8$ ). If we assume that *Calanus* can find and feed in rich microlayers (Mullin & Brooks 1972), then between-sample variability becomes im-

portant, and both the variability and the maxima of available chl *a* continued to increase from June through August (mean + SD = 1.12, 3.76, and 4.34 mg  $m^{-3}$ , respectively), according to the SeaWiFS estimates in Table 1 of Tarling et al. (2002). (2) Also, as an omnivore (Marshall & Orr 1955) *Calanus* may have been utilizing a seasonally increasing population of microzooplankton. (3) Finally, if food was not limiting, the increase in surface temperatures over this period probably meant that *Calanus* could search, feed and reach satiation more rapidly.

Animals in the leading edges of upwardly migrating layers have been observed by ADCP to ascend more slowly on average than the mean speed of the layer, whereas those on the bottom move up more quickly (Heywood 1996, Tarling et al. 2001). Such a pattern could be generated by differences in nutritive state (Pearre 2003), e.g. because some of the individuals in the leading edge had fed and started back down (Pearre 1974), while the bottom of the band has the largest proportion of hungry animals. This has yet to be investigated, and even if true, it would of course be only a temporary phenomenon. However, it would mean that ADCP returns could directly evidence satiation-cued descent.

Despite technical difficulties, the unresolved questions emphasize that more studies on this important subject are badly needed. I hope that the authors will continue along this line, and I look forward to further developments.

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#### LITERATURE CITED

- Buchholz F, Buchholz C, Reppin J, Fischer J (1995) Diel vertical migration of *Meganctiphanes norvegica* in the Kattegat: comparison of net catches and measurements with acoustic Doppler current profilers. *Helgol Wiss Meeresunters* 49:849–866
- Durbin EG, Campbell RG, Gilman SL, Durbin AG (1995) Diel feeding behavior and ingestion rate in the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. *Cont Shelf Res* 15:539–570
- Flik BJG, Ringelberg J (1993) Influence of food availability on the initiation of diel vertical migration (DVM) in Lake Maarsveen. *Arch Hydrobiol Beih Ergebn Limnol* 39: 57–65
- Gauld DT (1953) Diurnal variation in the grazing of planktonic copepods. *J Mar Biol Assoc UK* 31:461–474
- Heywood KJ (1996) Diel vertical migration of zooplankton in the northeast Atlantic. *J Plankton Res* 18:163–184
- Lass S, Tarling GA, Virtue P, Matthews JBL, Mayzaud P, Buchholz F (2001) On the food of northern krill *Meganctiphanes norvegica* in relation to its vertical distribution. *Mar Ecol Prog Ser* 214:177–200
- Manteyfel BP (1958) The vertical migrations of zooplankton

- eaten by fish and the food of planktophagous fish. (Author's abstract of lecture, November 25 1957) Byulletin' Moskovskogo Obshchestva Ispytatelei Prirody Otdel Biologiya 63:154–155
- Marshall SM, Orr AP (1955) The biology of a marine copepod *Calanus finmarchicus* (Gunnerus). Oliver & Boyd, Edinburgh
- Mullin MM, Brooks ER (1972) The vertical distribution of juvenile *Calanus* (Copepoda) and phytoplankton within the upper 50 m of water off La Jolla, California. In: Takeuchi AY (ed) Biological oceanography of the northern North Pacific Ocean and Bering Sea. Idemitsu Shoten, Tokyo, p 347–354
- Onsrud MSR, Kaartvedt S (1998) Diel vertical migrations of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. Mar Ecol Prog Ser 171:209–219
- Pearre S Jr (1974) Ecological studies of 3 West-Mediterranean chaetognaths. Invest Pesq 38:325–369
- Pearre S Jr (2000) Long term changes in diel vertical migration behavior: more ups and downs. Mar Ecol Prog Ser 197:305–307
- Pearre S Jr (2003) Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biol Rev 78:1–79
- Rey-Rassat C, Irigoien X, Harris R, Carloti F (2002) Energetic cost of gonad development in *Calanus finmarchicus* and *C. helgolandicus*. Mar Ecol Prog Ser 238:301–306
- Simard Y, Lacroix G, Legendre L (1985) *In situ* twilight grazing rhythm during diel vertical migrations of a scattering layer of *Calanus finmarchicus*. Limnol Oceanogr 30:598–606
- Simard Y, Lacroix G, Legendre L (1986) Diel vertical migrations and nocturnal feeding of a dense coastal krill scattering layer (*Thysanoessa raschii* and *Meganyctiphanes norvegica*) in stratified surface waters. Mar Biol 91:93–105
- Tarling GA, Buchholz F, Matthews JBL (1999) The effect of a lunar eclipse on the vertical migration of *Meganyctiphanes norvegica* (Crustacea: Euphausiacea) in the Ligurian Sea. J Plankton Res 21:1475–1488
- Tarling GA, Matthews JBL, David P, Guerin O, Buchholz F (2001) The swarm dynamics of northern krill (*Meganyctiphanes norvegica*) and pteropods (*Cavolinia inflexa*) during vertical migration in the Ligurian Sea observed by an acoustic Doppler current profiler. Deep-Sea Res I 48: 1671–1686
- Tarling GA, Jarvis T, Emsley SM, Matthews JBL (2002) Midnight sinking behaviour in *Calanus finmarchicus*: a response to satiation or krill predation? Mar Ecol Prog Ser 240:183–194

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