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REPLY COMMENT

Calanus finmarchicus descends in response to the arrival of krill — better unfed than dead

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The complexity of observing zooplankton behavioural ecology often makes it possible to derive several alternative interpretations of the same data set. Pearre (2003, this issue) has made a laudable attempt at reanalysing the data presented in Tarling et al. (2002) and putting forward some alternative explanations for the patterns observed by a 300 kHz acoustic Doppler current profiler (ADCP) moored during a summer period in the Clyde Sea. As he rightly suggests, further net samples and examination of stomach contents of *Calanus finmarchicus* would have been desirable in assisting this investigation. Nevertheless, some objections of Pearre (2003) suffer from misconceptions with regard to the nature of the acoustic data, whilst the remainder do not refute our principal hypothesis that the threat of predation from krill causes *C. finmarchicus* to descend in a synchronised fashion from the surface layers. We will outline the main pieces of evidence that led us to the above hypothesis and where the alternative explanations of Pearre (2003) do and do not hold.

The following pieces of evidence were the basis of the Tarling et al. (2002) study:

(1) Backscatter in the surface layers showed 2 major increases during the afternoon and evening, one of about 5 dB at 17:00 h, the other of about 15 dB at dusk (specifically, at the time when light levels were below 1 W m^{-2} and the relative rate of change of light was around 0.05 min^{-1}; Tarling et al. 2002, Fig. 6C).

(2) The larger increase corresponded to the arrival of the sound scattering layer (SSL) (Fig. 4, op. cit.), which was mostly made up of krill, as evidenced by corresponding net samples (Fig. 10, op. cit.). Further net samples indicated that the first peak was a result of *Calanus finmarchicus* arriving at the surface (Fig. 11, op. cit.), because at that time it was the only organism present in those layers capable of causing detectable backscatter.

(3) A period of downward velocities was observed soon after the arrival of the SSL. These velocities covered the depths between 20 m and 100 m and persisted for around 1 h (Fig. 5, op. cit.). Strong backscatter was not observed at the depths or times when these downward velocities were observed.

(4) Net samples showed that the majority of krill were too close to the surface at night to be potential contributors to the downward velocity band. The only depths where they could have contributed were between 20 and 50 m, but it is unlikely that they provide the dominant signal there, given that the ratio of *Calanus finmarchicus* to krill was 25:1. Below 50 m, where the magnitude and extent of the downward velocity band was particularly strong, there were no adult krill at all (Fig. 10, op. cit.). *C. finmarchicus* was the only organism found througout the entire depth range of the downward velocity band (20 to 100 m).

(5) This pattern persisted throughout the summer. The ascent of SSL always corresponded with dusk, which advanced during the study period. The timing of the downward velocity pattern shifted accordingly, and it always developed around 30 to 60 min after the SSL arrived.

From this evidence, it was concluded that:

***Calanus finmarchicus* was mainly responsible for the downward velocity pattern.** *C. finmarchicus* was the only acoustically detectable organism in net samples taken at the times and depths of the high downward velocities. The backscatter observed in the region of high downward velocities was between −80 dB and −75 dB. This level of backscatter was as low as that observed in the upper layer during late afternoon, when only *C. finmarchicus* was present. If, as Pearre (2003) suggests, krill contributed to this pattern, then (1) they would have been in the net samples taken at those times and depths and (2) they would have produced higher levels of backscatter.

As Pearre (2003) correctly points out, midnight sinking is a commonly reported behavioural trait in *Meganyctiphanes norvegica* (Simard et al. 1986, Buchholz et

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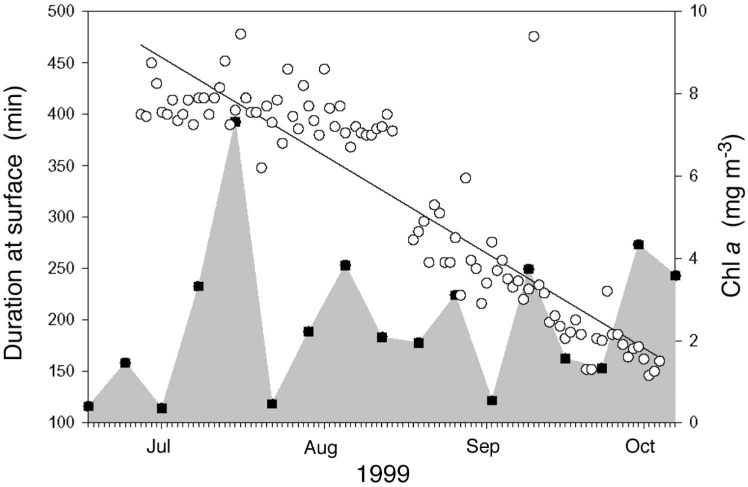

Fig. 1. *Calanus finmarchicus.* Comparison of (1) the duration spent at the surface before the synchronized decent and (2) levels of chl *a*, during the period from June 25 to October 3. Open circles: duration between the small rise in backscatter around 17:00 h and subsequent maximum downward vertical velocity; linear regression on these points (r^2 = 0.82) is shown. Black squares: SeaWiFS measurements of chl *a* (mg m^{-3}). Grey shading: linear interpolations between these points

al. 1995, Onsrud & Kaartvedt 1998) and Tarling et al. (1999, 2001) observed the phenomenon in the Ligurian Sea using a 150 kHz ADCP. In the Ligurian Sea studies, however, the downward vertical velocities were accompanied by an increase in backscatter. Furthermore, net deployments found *M. norvegica* at the times and depths where the downward velocities were observed. The absence of either an increase in backscatter or specimens in corresponding net samples counts against the possibility that *M. norvegica* was responsible for the downward velocities observed by Tarling et al. (2002).

***Calanus finmarchicus* fed in the upper layers during the early night for a duration that decreased linearly from June to August. Food concentration varied nonlinearly over the same period.** Fig. 7 in Tarling et al. (2002) shows that this decrease in time was relatively linear over the 3 mo study period. The amount of chl *a* in the water column (using SeaWiFS data as a proxy) did not increase linearly over the same period (Table 1, op. cit.). Pearre (2003) used the data in Table 1 of Tarling et al. (2002) to propose the opposite, i.e. that food concentration did increase over this period. He added variance to the mean for each study period to claim that the maxima were lowest in June and highest in August. Such a calculation is not justifiable, given the nature of the data set. The variance was based on the daily amount of chl *a* in the surface waters during the 6 days over which the acoustic data were averaged. It had no relationship to the variance through the water column, which was implied by Pearre (2003), and so neither supports nor rejects any argument relating to the ability of *C. finmarchicus* to feed on 'rich microlayers'.

To help clarify the true nature of the dataset, Fig. 1 presents the full sequence of chl *a* measurements over the period 25 June to 3 October. Superimposed is the theoretical time spent by *Calanus finmarchicus* in the surface layers i.e. the period between the time of the first small (5 dB) rise in backscatter at the surface and the subsequent time of the maximum downward velocity. It can be seen that there was no match between the trends in the chl *a* levels and the period of surface occupation by *C. finmarchicus*. Therefore, a direct relationship between the timing of synchronised descent and food concentration seems very unlikely. It was on this basis that we rejected the hypothesis that satiation was the main cause of the synchronised descent by *C. finmarchicus*.

Pearre (2003) considered that the net-catch data presented in Fig. 11 were a major challenge to our hypothesis. The figure was designed principally to show that *Calanus finmarchicus* arrived in the surface layer (0–20 m) in the late afternoon whilst krill did not arrive until around dusk. This allowed us to identify the taxa responsible for the 2 respective increases in backscatter at the surface during the afternoon and evening. On their own, the resolution of the net-sampling was too coarse to give any insight into the exact timings of when krill arrived and when *C. finmarchicus* descended, which is why our approach was, principally, to use net-samples as a means of determining the composition of the acoustic layers. Once the layers were identified, the 2 min by 8 m resolution of the acoustics was a much superior guide to the patterns of upward and downward migration. Contrary to the opinion of Pearre (2003), the compositions of the net samples presented in Fig. 11 of Tarling et al. (2002) are entirely consistent with our interpretation of the sequence of events in the acoustic patterns. In late August, the SSL arrived just before 20:00 h (Fig. 4C, op. cit.) whilst the period of high downward velocity started around 20:30 h (Fig. 5C, Tarling et al. 2002). The net samples presented in Fig. 11 (op. cit.) were completed at 09:49, 18:04, 20:42 and 02:38 h. The sample taken during the day was low in both *C. finmarchicus* and krill whilst, by 18:04h, numbers of *C. finmarchicus* but not krill had increased dramatically. Krill arrived in the surface layers by 20:42 h, consistent with the arrival of the SSL an hour earlier. Meanwhile, numbers of *C. finmarchicus* had fallen, which would be expected given that the downward velocity pattern began at 20:30 h. The data do not show that *C. finmarchicus* levels dropped before the arrival of the krill. A better presentation of Fig. 11 (op. cit.), omitting the linear interpolations, might have avoided the mistaken extrapolations of Pearre (2003).

We do not consider that the presence of CV individuals at depth during the course of the night is evidence of the early descent of satiated individuals. Marshall & Orr (1955) described the life cycle of *Calanus finmarchicus* in nearby Loch Striven. By mid to late summer, much of the population was a mixture of second and third generation individuals. The majority of the third generation arrested their development at the CV stage and remained in deep water until the following spring. Marshall & Orr (1955) supposed that these individuals had entered diapause. Hirche (1983) has since shown that such individuals do not feed, but minimise their respiration rate and meet residual metabolic demands through utilising oil sac reserves. Although physiological examinations were not carried out in the Tarling et al. (2002) study, it is highly likely that the non-migrating deep living individuals were in diapause.

Synchronised descent of *Calanus finmarchicus* was in response to the arrival of krill. Having excluded satiation as a cue for synchronised descent, 2 further possibilities are: (1) a reaction to light and (2) the arrival of predators. It is difficult to distinguish between these 2 possibilities on logical grounds alone, given that the SSL always arrived at the same point in the light cycle and *C. finmarchicus* always descended at around 30 min after this point. However, the light levels at the time of descent were negligible and probably insufficient as a proximal cue. The overlap of krill and *C. finmarchicus* in the surface layers would have lasted around 30 min, in which time the 2 species would have encountered each other. Therefore, the presence of krill as both a proximal and ultimate cue for a rapid descent stands as the most likely explanation. Even if such encounters do not take place, and krill are not a proximal cue, the close coupling between krill arrival and *C. finmarchicus* descent suggests that, ultimately, those individuals that timed their descent to maximise food intake and to avoid krill would have the greatest fitness and be more likely to contribute to the next generation.

We would like to make an important distinction between a synchronised descent and a vertical flux of individuals. The data presented did not discount that there was a flux of individuals between deep water and the surface any time between late afternoon and dawn. Even in late August, when there were just 3 h between 17:00 h and the arrival of the SSL, there should have been ample time to achieve satiation, given that gut filling time should be around 60 min (Wang & Conover 1986). Animals may have been constantly migrating up and down during that period or remaining in the same depth layer and resting whilst gorged.

We do not think that Pearre (2003) is objecting to all of the suggestions by Tarling et al. (2002). We observed synchronised nighttime descent, most likely as a response to the arrival of unsatiated krill. We are not discounting satiation as another important reason for the migration of *Calanus finmarchicus* individuals up and down, causing a vertical flux within the population. This would result in a spreading of the entire population over the water column and the creation of both upward and downward vertical velocities. This would not be discerned as a distinct pattern by the ADCP since the opposing velocities would be averaged out to zero by the firmware of the instrument. For a synchronised descent to be observed, the vast majority of the particles must have been moving in the same direction. The consistent appearance of this pattern indicates that, in addition to any possible vertical flux caused by hunger and satiation, there must have been another behavioural response that overrode the instinct to 'eat and run'. In this instance, the whole population 'ran', whatever the state of hunger each individual was in. The close temporal coupling between the arrival of krill and the synchronised descent of *C. finmarchicus* suggests that, in this instance, the threat from hungry krill induced the response.

It is unclear how widespread the phenomenon of a synchronised nighttime descent may be. The fact that Gauld (1953), whose study was also based in the Clyde Sea, did not find any mass transfer of *Calanus finmarchicus* emphasises the limitations of net sampling in this regard. The observations of Tarling et al. (2002) with long-term acoustics suggests that more vertical migration patterns may exist than have been previously noticed. The case of a subsequent dawn rise by this species, as observed by Simard et al. (1985) in the St. Lawrence estuary, is an interesting further consideration. It is true that *C. finmarchicus* would be migrating into the same predatory field that they had avoided earlier in the night. However, as found by Lass et al. (2001), krill would have been feeding the whole night on other prey items, including phytoplankton and small copepods. Arriving at the surface when the predators are almost gorged would be the next best thing to arriving when they are not there. Tarling et al. (2002) did not take net samples during the dawn period to discover whether this phenomenon was common also in the Clyde Sea, but it is clear from the acoustics that any rise was not a synchronised event. Re-ascent is likely to be induced by hunger, and those individuals that are starved may be more prepared to take risks and rise earlier than those that are replete. At the population level therefore, it is most likely that the rise would be a gradual process, which would make it indistinct acoustically.

We agree wholeheartedly with Pearre (2003) that more studies in this important subject area are badly needed. A greater frequency of net sampling would discern whether a dawn rise did take place. Examination of gut contents would distinguish which parts of the population migrated and which did not. More importantly, well-timed net sampling would be able to determine the gut fullness of individuals at the time of the synchronised descent. We would expect a great deal of variability in feeding state between individuals if their descent was a means of rapid escape. We certainly hope to continue our investigations in this regard.

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