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What drives the diel vertical migrations of Antarctic midwater fish?

Bruce H. Robison

Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA. E-mail: robr@mbari.org

Like their counterparts at lower latitudes, many Antarctic midwater fish make extensive, diel vertical migrations. However, Antarctic species make these migrations in the absence of two of the three selective advantages generally ascribed to this behaviour. Because the water column is nearly isothermal, there is no metabolic bonus to be gained from thermal differences in habitat depth. Likewise, because their prey do not perform significant vertical migrations, the fish migrations act to diminish rather than enhance their feeding opportunities. For Antarctic midwater fish, the sole advantage of these migrations appears to be the avoidance of visually-cued predators in the upper part of the water column. An evaluation of the relative importance of the three selective factors supports the suggestion that predator avoidance may also be the principal driver of diel vertical migrations for midwater fish at lower latitudes.

INTRODUCTION

Morning and evening vertical migrations by midwater fish are a regular feature of oceanic communities worldwide. In terms of biomass and the number of individuals involved, they must be the largest vertebrate migrations on earth. The micronektonic fish that undertake these migrations are principal consumers of herbivorous zooplankton at the third trophic level of oceanic ecosystems. In turn, they constitute a primary forage resource for larger fish, squid, birds, and marine mammals at the fourth trophic level. By day this group of fish occupies the mesopelagic portion of the water column, at depths from about 200 to 800 m, where light levels and temperatures are low. At dusk they move upward, and most of them spend the night feeding in warmer waters near the surface (Marshall, 1979).

The timing and extent of the vertical migrations by midwater fish appear to be linked to similar movements by their zooplankton prey (Merrett & Roe, 1974; Marshall, 1979). Thus the most obvious explanation for the fish migrations has been that they are simply following their food. Two additional selective advantages have been proposed. The first suggests that their metabolic rates are significantly reduced and thus that energy is conserved by the descent to colder depths after feeding (McLaren, 1963; Enright, 1977; Marshall, 1979). The second suggests that the return to darker waters during the day, reduces mortality from visually-cued predators, active near the surface (Childress, 1995). While all three of these advantages may accrue to some vertically migratory fish, their relative importance as selective factors has never been determined experimentally.

Each of the three presumed selective advantages depends upon a specific property of the habitat: (i) the abundance and migratory behaviour of prey; (ii) the temperature differential of the water column; and (iii) the presence of visually-cued predators near the surface. Oceanic waters around Antarctica provide a natural experiment to examine the relative significance of these factors. In the Antarctic, natural conditions eliminate the potential advantages of metabolic gain and prey proximity. The results of vertical distribution studies in these waters offer clear evidence that predation pressure alone is sufficient to drive the diel vertical migrations of midwater fish.

MATERIALS AND METHODS

This study was conducted aboard the RV 'Hero' during February, 1982 and March–April, 1983, in two deep basins beneath the Croker Passage, west of the Antarctic Peninsula (64°05′S 61°48′W). Thirty-five discrete-depth net hauls were made with an opening–closing midwater trawl that had a mouth area of 4.8 m^2 and a mesh size of 4.5 mm. Suspended in the mouth of the main trawl was a fine mesh (162 μm) plankton net with a mouth opening of 0.75 m^2. Both nets were opened and closed at the mouth by mechanical timers. The volume of water filtered while trawling was determined by paired flowmeters, and sampling depths, which covered the upper 1000 m of the water column, were measured by an *in situ* time–depth recorder. Trawling speed was 2.5 knots. Vertical profiles of temperature vs depth were measured routinely throughout the trawling programme. Methods of trawling and determining catch abundance are detailed in Hopkins (1985a,b), along with a description of the area sampled. Because of the hazardous conditions associated with trawling from a small vessel in ice-filled waters, the precision of the vertical sampling intervals was not as good as might be obtained in ice-free waters. Nevertheless, the results on vertical distribution and migration for these species are entirely consistent with those in the literature from other regions of the Antarctic (Lancraft et al., 1989, 1991). Observations of seabird and marine mammal abundance were made throughout the diel trawling cycle.

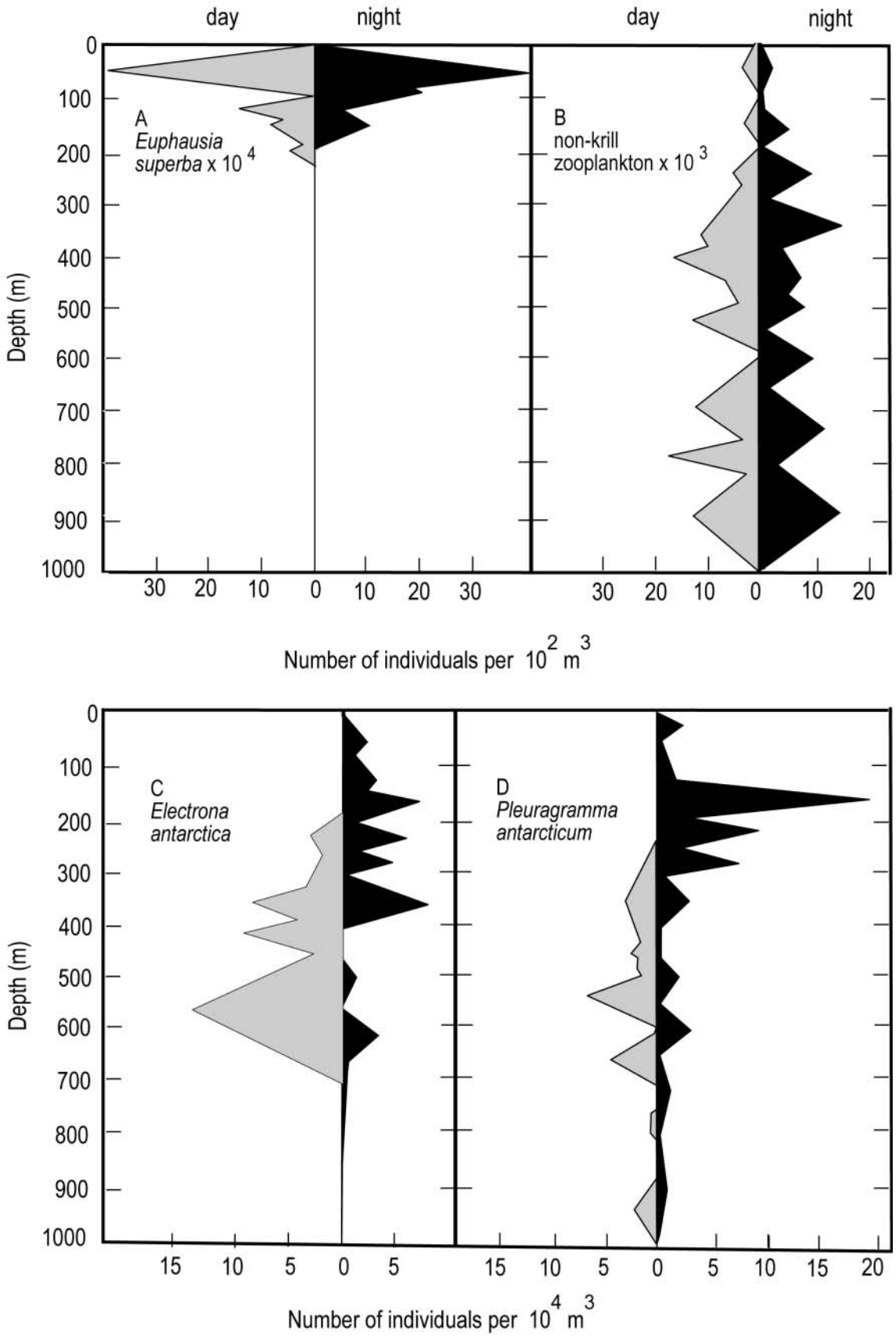

Figure 1. Diel vertical distribution patterns of: (A) krill, *Euphausia superba*; (B) non-krill zooplankton; (C) the myctophid fish *Electrona antarctica*; and (D) the notothenid fish *Pleuragramma antarcticum*; in deep basins beneath the Croker Passage, Antarctica (maximum bottom depth=1250 m). The area of the triangles indicates the percentage of the total population found within each sampled depth interval, and their lateral extent shows absolute abundance, normalized for the volume of water filtered at each depth interval. Note the scale change between upper and lower panels. Because individual krill are much larger than the non-krill zooplankters, the biomass of prey (80% krill) was greatest in the upper 100 m. Fish and krill data are from the trawl collections, zooplankton are from the plankton net.

RESULTS

The water column over the basins was nearly isothermal, with an average temperature of 0.5°C and a mean temperature differential of less than 1°C between the surface and a depth of 800 m (Hopkins, 1985a). Krill, *Euphausia superba* Dana, strongly dominated the pelagic fauna of the basins by accounting for more than 80% of the zooplankton biomass (Hopkins, 1985a). Vertical distribution profiles show that the bulk of the krill populations remained in the upper 100 m both day and night (Figure 1A). Copepods, which made up most of the remaining zooplankton, occurred chiefly in the deeper reaches of the water column and also showed no substantial diel movements (Figure 1B). Foraging seabirds, primarily Adelie penguins, *Pygoscelis adeliae* (Hombron & Jacquinot, 1841), and a variety of petrels were abundant in Croker Passage (Obst, 1985). Likewise, crabeater seals, *Lobodon carcinophagus* (Hombron & Jacquinot, 1842), and fur seals, *Arctocephalus gazella* (Peters, 1875), were common along the bordering shorelines and in the water (Costa & Crocker, 1996).

In contrast to the static vertical distribution patterns of krill and copepods, the dominant midwater fish performed regular vertical migrations on a diel cycle. Two species, a myctophid, *Electrona antarctica* (Günther, 1878) and a nototheniid, *Pleuragramma antarcticum* Boulenger, 1902, accounted for 70% of the mesopelagic fish collected. Myctophids are quintessential vertical migrators, found throughout the world's oceans (Marshall, 1979), although *E. antarctica* is endemic to waters south of the Antarctic Convergence. *Pleuragramma antarcticum* and all other nototheniid fish are also restricted to high southern latitudes (DeWitt, 1971). By day, both fish species were absent from the upper 200 m, with *E. antarctica* centered at about 500 m (Figure 1C) and *P. antarcticum* slightly deeper, near 550 m (Figure 1D). At night both fish species re-occupied the upper 200 m of the water column, with peaks of abundance at about 150 m and 200 m respectively. Because of the long days of the austral summer, the fish spent only about five hours in the upper part of their range each night. Daytime net avoidance is an unlikely reason for the observed pattern because the total abundance of both species throughout the water column was comparable, both day and night.

In terms of the three presumed selective factors, the 'experimental' conditions in the sampling area can be characterized as follows. There was no significant temperature differential across the vertical depth range of the principal migratory fish. Piscivorous seabirds and seals were locally abundant in the surface waters throughout Croker Passage. Zooplankton biomass was densely concentrated in the upper 100 m around the clock; and the dominant species of zooplankton made no large-scale migrations. Under these atypical conditions, Antarctic midwater fish exhibited diel vertical migrations typical of their counterparts in more temperate waters.

DISCUSSION

The case for prey proximity as a selective factor rests on the assumption that midwater fish migrate in order to remain close to concentrations of their prey, which are usually vertical migrators themselves (Marshall, 1979). In Croker Passage, krill were virtually the only prey consumed by migratory fish (Hopkins, 1985b). Krill were orders of magnitude more abundant than the fish and occurred almost exclusively in the upper part of the water column (Miller & Hampton, 1990). *Euphausia superba* appears to rely on schooling instead of vertical migration to avoid predation (Hamner et al., 1983). Thus the migratory behaviour of the fish worked counter to the hypothetical selective advantage of maintaining proximity to prey, by regularly separating the fish from their principal food source. Furthermore, the short duration of the night-time feeding periods enhanced this negative effect.

The case for metabolic gain as a result of diel vertical migrations is based on the assumption that metabolic rates are reduced by the lower temperatures encountered at depth during the day (McLaren, 1963; Enright, 1977). In a typical temperate water column there is a 10°C drop in temperature across the upper 800 m. However, the known respiratory rates of temperate and Antarctic midwater fish are such that the slight (1–3°C) temperature differential in Antarctic waters, could not be metabolically significant (Torres & Somero, 1988). Thus for Antarctic midwater fish, temperature differential cannot be a significant factor in their migrations.

The case for predation pressure as a selective factor in diel vertical migrations is based on the assumption that visually-cued predation is diminished when the fish remain in dark waters. This case is well supported by the data on Antarctic species. In Croker Passage the principal predators of fish and krill were penguins, which are active only in daylight hours, during which they dive to depths as great as 250 m or more in pursuit of prey (Croxall & Prince, 1980; Obst, 1985). At night, the dominant fish- and krill-eating birds were petrels, which feed chiefly at the surface (Croxall & Prince, 1980). Both of the seal species common in Croker Passage feed on krill and fish during shallow (30–40 m) dives made mostly at night (Costa & Crocker, 1996). During the day the fish were deep in the water column, well beyond the depth range of predatory seabirds. At night when the deep-diving birds were roosting, the fish returned to the upper layers; albeit still below the foraging depths of the nocturnal petrels and seals, and below the bulk of the krill population. At these depths krill density is below the threshold where schooling is an effective deterrent to predation.

With temperature and prey distribution eliminated as contributing factors, the present results support the hypothesis that reduced predation from visually-cued predators is the principal selective advantage derived by Antarctic midwater fish from their diel vertical migrations. One might argue that the migrations of Antarctic species are merely a relict behaviour pattern, retained from ancestral stocks that evolved at lower latitudes. This possibility is refuted by the distinct migratory behaviour of *Pleuragramma antarcticum* (Figure 1D), a pelagic member of the chiefly benthic family Nototheniidae, which almost certainly originated in Antarctic waters (DeWitt, 1971).

It might also be argued that results obtained in the semi-isolated basins beneath Croker Passage do not represent conditions in more oceanic waters around the Antarctic continent. However, the general environmental conditions of thermal structure, predation pressure, and vertical prey distribution reported here, also prevail in the open waters

of the Scotia and Weddell Seas (Lancraft et al., 1989), and in waters below the margins of pack ice (Lancraft et al., 1991). In these regions, most of the midwater fish are diel vertical migrators, and their visually-cued predators commonly forage to daytime depths of 400 m or more (Kooyman & Ponganis, 1997). The case for predation pressure is also supported by studies of vertical migration patterns beneath the seasonal ice pack. Midwater fish migrate much closer to the surface when surface-foraging seabirds are excluded by the winter/spring ice pack, although they are still linked to the diel light cycle (Kauffman et al., 1995). These results suggest that during the austral winter the vertical extent of daytime migrations may be reduced, thus increasing proximity to prey during the leanest and darkest season, but data from winter are lacking.

While there may be other explanations for these migrations, none are evident here or in the literature. If we consider the three principal hypotheses that have been generally applied to midwater fish, there can be little doubt that predation pressure drives the diel vertical migrations of *Electrona antarctica* and *P. antarcticum* in the Antarctic. In non-polar regions the situation is more complex, because all three selective factors probably contribute to the adaptive value of diel migrations. However, given the present results from Antarctica, it now seems possible to make a rough approximation of their relative importance in simple energetic terms.

Most vertically migratory fish do most of their feeding near the surface at night (Marshall, 1979), which readily explains their upward movements. The fundamental question then is: why do they migrate downward during the day? In temperate species the metabolic gain derived from occupying deeper, colder water is estimated to be less than 2% of the energetic value of the daily food ration (Torres et al., 1979). This 'energy bonus' alone is insufficient compensation for the estimated 10–20% of the daily ration that is expended during the migrations (Childress, 1995). Maintaining proximity to prey throughout the diel depth range would appear to offer a much stronger energetic advantage than temperature differential. The potential energetic value of maintaining sufficiently close proximity to feed on migratory prey throughout the diel cycle, could easily double the daily food ration. However, most migratory fish succeed with only nighttime feeding (Marshall, 1979). Field tests and manipulative experiments (Bollens et al., 1992) have shown that for zooplankton, diel vertical migration is chiefly a predator avoidance behaviour, and that the only unifying concept in understanding the myriad patterns of zooplankton migration is visual predation. The fact that predation pressure can drive Antarctic midwater fish away from their food source, even when the nights are very short, is strong evidence that it may also be the principal selective factor in the diel vertical migrations of midwater fish at lower latitudes as well.

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