NOTE

Schooling of the vertically migrating mesopelagic fish Maurolicus muelleri in light summer nights

Stein Kaartvedt^{1,*}, Tor Knutsen², Jens Christian Holst²

¹Department of Biology, University of Oslo, PO Box 1064 Blindern, N-0316 Oslo, Norway ²Institute of Marine Research, PO Box 1870, N-5024 Bergen, Norway

ABSTRACT: Vertically migrating *Maurolicus muelleri* arrested their nocturnal ascent below the peak zooplankton concentrations during light summer nights at 62°N. At 69°N, the behavior was further modified, with *M. muelleri* forming schools in the upper layer at night. We suggest that *M. muelleri* used schooling as an antipredator strategy due to the absence of dark periods.

KEY WORDS: Planktivorous fish \cdot Acoustic scattering layer \cdot DVM \cdot Midnight sun

Organisms at high latitudes must cope with extreme light conditions. Waters north of the Arctic circle are characterized by midnight sun in summer and continuous darkness in winter. This certainly affects both feeding opportunities for visual predators (e.g. Suthers & Sundby 1996) and risk of predation. In this note, we address the diel vertical migration (DVM) behavior of the mesopelagic planktivorous fish *Maurolicus muelleri* (Müllers pearlside) in the absence of dark nights during summer.

DVM provides a trade-off between catching food and avoiding predators (Clark & Levy 1988). In Norwegian waters, the daytime depth of *Maurolicus muelleri* varies between ~50 and 200 m, depending on fish size and light conditions (e.g. Giske et al. 1990, Baliño & Aksnes 1993, Kaartvedt et al. 1996). Vertically migrating individuals exploit shallow zooplankton concentrations at dusk and dawn, when light intensities are sufficient for visual predation on plankton, but acceptably low for protection against predation by visually hunting piscivores (so-called 'antipredation windows'; Clark & Levy 1988, Rosland & Giske 1994, 1997). *M. muelleri* generally spends the night between these

As nights become less dark, the optimal vertical distribution for simultaneously catching food and avoiding predators is altered. We studied the DVM behavior of *Maurolicus muelleri* at 2 locations in the summer of 1993; from 4 to 12 June in Storfjorden, western Norway (62° 2′ N, 6° 3′ E) and from 3 to 4 August in the Norwegian Sea (69° N, 9.4° E). Fish distribution was mapped by SIMRAD EK 500, 38 kHz echo sounders, and target identification was done by Harstad trawl (Nedreaas & Smedstad 1987) and Åkra trawl (Valdemarsen & Misund 1995).

In Storfjorden, we observed dielly migrating scattering layers (SL; Fig. 1) that appeared to consist almost exclusively of *Maurolicus muelleri*. Of 5 tows with Harstad trawl aimed at the SL during different phases of the diel cycle, *M. muelleri* on average constituted 95% of the fish catches by weight (100, 100, 100, 96, 78%), with a maximum catch of 94 kg *M. muelleri* nautical mile⁻¹. One tow directed above the SL resulted in no *M. muelleri*. The only other major group represented in the catches was jellyfish, with a maximum catch of 15 kg nautical mile⁻¹, obtained in a tow between 39 and 50 m.

Maurolicus muelleri ascending from a mid-day depth of 150 to 200 m never migrated to the surface at night, but aggregated at about 20 to 40 m (Fig. 1). They thereby excluded themselves from the higher standing stock of potential zooplankton prey in the uppermost 12 m (revealed by concurrent sampling; Skjoldal et al. 1993), though they migrated into waters characterized by maximum relative fluorescence and intermediate zooplankton abundance (Skjoldal et al. 1993). Hydrographic gradients from 20 to 12 m (34.4 to 32.6 psu and 8.1 to 8.9°C) should not represent a barrier to further

periods at subsurface depths (Giske et al. 1990, Giske & Aksnes 1992, Baliño & Aksnes 1993, Goodson et al. 1995, Torgersen et al. 1997).

^{*}E-mail: stein.kaartvedt@bio.uio.no

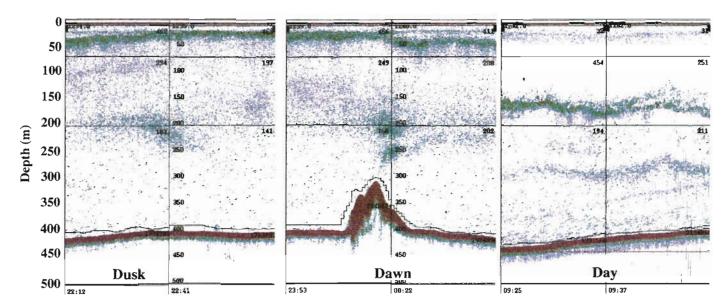


Fig. 1. Vertical distribution of Maurolicus muelleri in summer illumination at 62° N. Echogram (EK500, 38 kHz) obtained by RV 'Johan Hjort' in Storfjorden, western Norway from 6 to 7 June 1993 by day, dusk/night and night/dawn. The distribution of the scattering layer did not change during the intermediate night period not shown in the figure. Times are GMT. Color scale (see Fig. 2) refers to volume backscattering strength (dB). Vertical lines delineate nautical miles. Digits in upper right corners give integrated echo levels (S_A) for the outlined 'blocks', calculated by the Bergen Echo Integrating system (Foote et al. 1991)

upward migration, as *M. muelleri* is observed to cross corresponding, and even stronger gradients (Baliño & Aksnes 1993, author's unpubl. results). Hence, we suggest that the ascent ceased because of the light summer night.

Nighttime surface light values varied between ~1 and 10 μ mol m⁻² s⁻¹ (measured by a Li-Cor quantum sensor), and about 3% of the surface light reached 20 m. The estimated nocturnal light intensities at the top of the scattering layer (~ 0.3 to 3×10^{-1} µmol m⁻² s⁻¹) correspond to previously published maximum values experienced by vertically migrating Maurolicus muelleri when they arrive in surface waters at dusk (Rasmussen & Giske 1994, Rosland & Giske 1994, Bjelland 1995). Therefore, these light values would allow visual feeding throughout the night. Accordingly, no midnight sinking was observed (Fig. 1), in concordance with results by Rasmussen & Giske (1994) for May, but in contrast to studies carried out during darker periods of the year (see previous references). Although echograms selected from only 1 night are presented in Fig. 1, the distribution of M. muelleri was studied throughout 6 nights between 4 and 12 June, and similar distributions were observed each night.

At even higher latitudes, days become longer and summer nights even less dark (though there still is a marked diel change in light levels), with periods of midnight sun north of 67.3° N. This may imply absence of antipredation windows when planktivores can harvest the food sources of upper waters while remaining

sheltered against piscivores. One consequence might be that vertically migrating organisms (like *Maurolicus muelleri*) cannot enter the upper, productive layers through several summer months. The light cycle might thus actually constrain the geographic range where vertically migrating species could prosper (Sameoto 1989). Alternatively, they may alter their antipredator behavior, making harvesting of the plankton in the continuously illuminated upper layers possible. Schooling appears to be the appropriate antipredator strategy for the Antarctic krill *Euphausia superba* during southern polar summers (Lancraft et al. 1989, Hamner 1996), and schooling tends to increase among planktivorous fish when exposed to danger of predation (Magurran 1990).

This indeed seems to be the case for *Maurolicus muelleri*. At 69° N in the Norwegian Sea, we obtained acoustic records of nocturnal schools near the surface, which we ascribe to *M. muelleri* (see below). These schools appear as red dots of the upper water layer (Fig. 2). Note that schools recorded from a moving vessel will appear particularly small in shallow waters due to the narrow acoustic beam close to the transducer (see Misund et al. 1996).

We made 1 tow with an Åkra trawl to identify these targets. The trawl was equipped with an inner net of 11 mm mesh size to retain small organisms, and flotation was used to restrict sampling to near the surface. In total, 212 kg *Maurolicus muelleri* were captured (75 kg nautical mile⁻¹), constituting 94% of the total

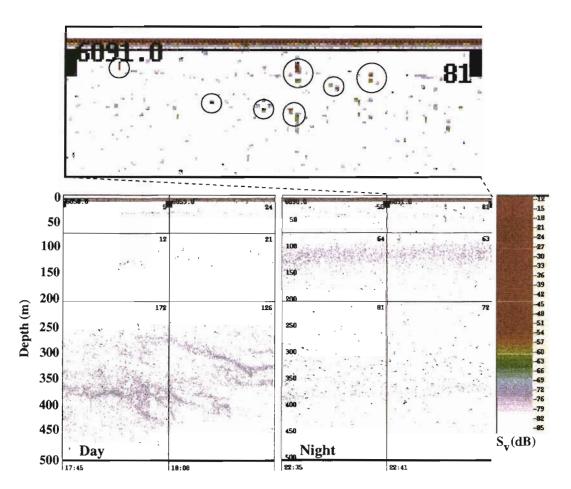


Fig. 2. Vertical distribution of *Maurolicus muelleri* in summer illumination at 69° N. Echogram (EK500, 38 kHz) from day and night from 3 to 4 August 1993 obtained by RV 'G.O. Sars' in the Norwegian Sea. Times are GMT. Color scale refers to volume backscattering strength (dB). Vertical lines delineate nautical miles. Digits in upper right corners give integrated echo level (S_A) for the outlined 'blocks', calculated by the Bergen Echo Integrating system (Foote et al. 1991). The upper 75 m of one nautical mile is expanded, and targets interpreted as schools by their strength/vertical extension are encircled

fish catch. Krill was the other major constituent in the catches, with 44 kg nautical mile⁻¹. Mackerel (*Scomber scombrus*; 9 captured individuals) had stomachs filled with *M. muelleri*.

We conclude that the schools consisted of *Maurolicus muelleri*. No 'typical' SL which could account for the high catches appeared in the echograms, nor did the trawl catch alternative targets possibly accounting for the acoustic records. Schools of herring form similar visual acoustic signatures, but normally result in much higher integrated echo levels (e.g. Misund et al. 1996).

The total abundance of *Maurolicus muelleri* in this case was much lower than in the example from Storfjorden (cf. the integrated echo levels given in Figs. 1 & 2), but the fish concentrations in the schools were higher than in the fjord (cf. the color code of the echoes). Our recordings (3 to 4 August) were done ~10 d after termination of the midnight sun period, but nights were still light.

The literature provides a few examples of daylight near-surface schooling of mesopelagic fish that normally carry out DVM (Alverson 1961, Marchal & Lebourges 1996). On both occasions, the fishes (Benthosema pterota and Vinciguerria nimbaria) were chased by tuna in waters near the equator (off the coast of Costa Rica and in the northern equatorial current, respectively). We speculate that schooling also in these cases may have been related to the local light regime. Like high latitudes, equatorial regions represent an extreme regarding light climate, in this case due to very swift switching between daylight and darkness. The short dusk and dawn periods imply short antipredation windows. Hence, in the morning the fishes could become rapidly exposed to diurnal predators. Schooling as a strategy to extend the feeding period in upper layers, or as an immediate defense response when encountered by predators, may then be benefiAcknowledgements. We thank H. R. Skjoldal and L. Postel for the use of data obtained during the ICES sea-going workshop on zooplankton methodology in Norway, June 1993. This is a contribution from TASC (Trans Atlantic Study of Calanus finmarchicus) funded by the European Commission. contract no MAS3-CT95-0039.

LITERATURE CITED

- Alverson FG (1961) Daylight surface occurrence of myctophid fishes off the coast of Central America. Pacif Sci 15:483
- Baliño BM, Aksnes DL (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Mar Ecol Prog Ser 102:35-50
- Bjelland O (1995) Life-history tactics of two fjordic populations of *Maurolicus muelleri*. Cand scient thesis, University of Bergen
- Clark CW, Levy DA (1988) Diel vertical migration by juvenile sockeye salmon and the antipredation window. Am Nat 131:271–290
- Foote KG, Knutsen HP, Korneliussen RJ, Nordbø PE, Røang K (1991) Postprocessing system for echo sounder data. J Acoust Soc Am 90:37–38
- Giske J, Aksnes DL (1992) Ontogeny, season and trade-offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri*. Sarsia 77:253-261
- Giske J, Aksnes DL, Baliňo BM, Kaartvedt S, Lie U, Nordeide JT, Salvanes AGV, Wakili SM, Aadnesen A (1990) Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. Sarsia 75:65–82
- Goodson MS, Giske J, Rosland R (1995) Growth and ovarian development of *Maurolicus muelleri* during spring. Mar Biol 124:185–195
- Hamner WM (1996) Predation, cover, and convergent evolution in epipelagic oceans. In: Lenz PH, Hartline DK, Purcell JE, Macmillan DL (eds) Zooplankton: sensory ecology and physiology. OPA, Amsterdam, p 17–35
- Kaartvedt S, Melle W, Knutsen T, Skjoldal HR (1996) Vertical distribution of fish and krill beneath water of varying optical properties. Mar Ecol Prog Ser 106:51–58
- Lancraft TM, Torres JJ, Hopkins TL (1989) Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). Polar Biol 9:225-233 Magurran AE (1990) The adaptive significance of schooling

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

- as an anti-predator defense in fish. Ann Zool Fenn 27: 51-66
- Marchal E, Lebourges A (1996) Acoustic evidence for unusual diel behavior of a mesopelagic fish (Vinciguerria nimbaria), exploited by tuna. ICES J Mar Sci 53:443–447
- Misund OA, Aglen A, Hamre J, Ona E, Røttingen I, Skagen D, Valdemarsen JW (1996) Improved mapping of schooling fish near the surface: comparison of abundance estimates obtained by sonar and echo integration. ICES J Mar Sci 53:383–388
- Nedreaas K, Smedstad OM (1987) Abundance and distribution of postlarvae in the 0-group saithe survey in the North Sea and the Northeast Arctic in 1986 and 1987. ICES CM 1987/G:31
- Rasmussen Ol, Giske J (1994) Life-history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. Mar Biol 120:649–664
- Rosland R, Giske J (1994) A dynamic optimization model of the diel vertical distribution of a pelagic planktivorous fish. Prog Oceanogr 34:1-43
- Rosland R, Giske J (1997) A dynamic model for the life history of *Maurolicus muelleri*, a pelagic planktivorous fish. Fish Oceanogr 6:19–34
- Sameoto D (1989) Feeding ecology of the lantern fish *Benthosema glaciale* in a subarctic region. Polar Biol 9:169–178
- Skjoldal HR, Wiebe P, Knutsen T, Postel L (1993) Preliminary report from the sea-going workshop in Norway June 1993 on intercomparison and evaluation of methods for sampling and determination of zooplankton distribution and biomass (ICES study group on zooplankton production). ICES CM 1993/L:45
- Suthers IM, Sundby S (1996) Role of midnight sun: comparative growth of pelagic juvenile cod (*Gadus morhua*) from the Arcto-Norwegiān and a Nova Scotian stock. ICES J Mar Sci 53:827–836
- Torgersen T, Kaartvedt S, Melle W, Knutsen T (1997) Large scale distribution of acoustical scattering layers at the Norwegian continental shelf and the eastern Norwegian sea. Sarsia 82:87–96
- Valdemarsen JW, Misund OA (1995) Trawl design and techniques used by Norwegian research vessels to sample the pelagic zone. In: Hylen A (ed) Precision and relevance of pre-recruit studies for fishery management related to fish stocks in the Barents Sea area and adjacent waters. The sixth Norwegian-Russian symposium, Bergen, 14–17 June 1994. Institute of Marine Research, Bergen, p 135–144

Submitted: February 9, 1998; Accepted: July 17, 1998 Proofs received from author(s): August 10, 1993