Intraspecific variation in vertical distribution, timing of vertical migration, and colouration of the mesopelagic shrimp Sergestes arcticus were studied in the >400 m deep part of Masfjorden, Norway. Very few individuals were caught in the upper strata during daytime, and larger individuals occurred deeper during the day than smaller ones. Vertical migration was prominent and no overall trend of increasing length with depth was found at night. Small individuals arrived in the upper layers earlier than larger ones. Animal colouration assessed by digital photography revealed significant variance in individual redness. Depth of capture was the most important factor explaining colouration, with increasing degree of redness with depth. Assessing the gut fullness of the transparent shrimps provided a rapid way of estimating feeding activity and showed that feeding took place mainly at night.

INTRODUCTION

In the upper pelagic habitat, visual predators flourish; places to hide are almost non-existent and other means are necessary to become inconspicuous. One essential characteristics of pelagic habitat is the changing light conditions with depth and time. And as light conditions in the water column change, so do the optimal anti-predation mechanisms (Johnsen, 2002). For a given species, this may be reflected in size by depth and time, feeding by depth and time, and colour by depth and time.

It is well established that sizes of organisms generally increases with depth, both within and between species [e.g. euphausiids and copepods (Wiebe et al., 1992), shrimps (Buskey et al., 1989), and fishes (Giske et al., 1990)]. This is commonly explained as a result of smaller individuals being less visible than larger ones and therefore they can occupy the more illuminated shallower waters at lower risks than larger individuals would face (e.g. Giske et al., 1990).

Diel vertical migration (DVM) whereby pelagic species seek cover in deep dark water during daytime and only enter the risky upper layers to feed at night-time is another way to avoid predators (Hays, 2003). DVM is now widely studied, however mainly with a focus on main population movements. Asynchronous migrations, whereby organisms may spend short periods only in upper waters, have been less studied, yet have been derived from identification of surface prey organisms in the stomachs of predators captured at depth (Pearre, 2003) and recently documented by studies of individual jellyfish in situ (Kaartvedt et al., 2007).

Diel feeding rhythms in themselves, with feeding limited to periods of darkness, also reduce conspicuousness. This is because the search activity may expose organisms to predators (Wright and O’Brien, 1982; Tiselius and Jonsson, 1997), and because food in the gut of an otherwise transparent animal would make it more vulnerable to visual predators in light (Pearre,
1973; Bollens and Stearns, 1992; Giske et al., 1994; Tsubo et al., 1998).

Camouflage is another widespread predator avoidance strategy that may be achieved by small size, transparency, photophore-mediated counter-illumination, and cryptic colouration (Johnsen, 2002 and references therein). Colouration has been qualitatively assessed on several occasions, but only seldom quantified (Vestheim and Kaartvedt, 2006). Yet the main patterns seem to be established. During daytime, in well illuminated epipelagic layers, no colouration at all is the best solution (Johnsen, 2001a) and epipelagic invertebrate species are generally reported to be colourless and transparent. However, in deeper layers with a light regime characterized by weak, downwelling parallelized blue light (Jerlov, 1968) and bioluminescent flashes, red, purple or black colouration may be more beneficial because it helps in avoiding surface reflection (Widder et al., 1983; Johnsen, 2001a). Being pigmented rather than transparent is probably also metabolically cheaper (e.g. McFall-Ngai, 1990; Johnsen, 2001b). Mesopelagic species are accordingly often half-red (reddish colouration of guts and opaque tissue) and bathypelagic species are uniformly red, purple or black (e.g. Hardy, 1956; Herring and Roe, 1988). But both diel vertically migrating animals and animals remaining at the same depth by day and night may achieve better camouflage by altering their colouration (Johnsen and Sosik, 2003) and at night-time, some colouration might be better also in the upper layers (Johnsen, 2002).

Shrimps belonging to the genera Sergestes are often abundant mid-water macrouric crustaceans in marine pelagic communities and the species Sergestes arcticus is an important constituent of the North Atlantic ecosystem (e.g. Omori and Gluck, 1979; Gislasen et al., 2007). They are common among mesopelagic species, their vertical distribution may span several hundreds of metres and they are extensive vertical migrants (e.g. Flock and Hopkins, 1992). They are known to feed mainly carnivorously, preferring small crustaceans as prey, particularly copepods (Judkins and Fleminger, 1972; Flock and Hopkins, 1992). Sergestes has large chromatophores and it is noted that they should have the ability to vary their level of colouration and thereby optimize its cryptic function to depth and time (Foxton, 1970). In this paper, we assess the size by depth, including timing of vertical migrations of different size classes, diel feeding patterns and colouration of Sergestes arcticus. By applying depth and time-integrated trawling and digital photography in combination with standard enumeration methods, we examine in situ how fitness in one species can be achieved through these varieties of adaptations and strategies and explore the degree of intraspecific variation.

METHOD

Sampling

Sampling was carried out from the RV Trygve Braarud at a >400 m deep location (60° 52.45’N, 5° 25.06’E) in Maelfjorden, western Norway, on 04–05 October 2006. Sergestes arcticus is known to be the dominant larger mesopelagic crustacean species in this fjord (Kaartvedt et al., 1988). Salinity, temperature, fluorescence and organic matter were measured by CTD. To assess the distribution of potential prey, mesozooplankton was sampled by a WP2 net (200 µm mesh size) hauled vertically at 0.5 m s⁻¹ and closed at preselected depths with a Nansen releaser activated by a drop messenger. Two series were taken during daytime in the depth intervals 400–300, 300–200, 200–100, 100–50 and 50–0 m. The samples were preserved in 4% buffered formalin for later analysis and enumeration. Before analysing, the samples were split using a LEA plankton divider (Wiborg, 1951) and one-tenth was enumerated with all animals being counted and identified, if possible, to genus.

Sergestes arcticus

Sergestes arcticus was sampled with a ~100 m² pelagic trawl equipped with a Scanmar multisampler opening/closing device attached to the rear end of the trawl, permitting depth stratified sampling in 3 depth or time intervals per tow. Mesh size near the opening was 20 cm, declining to 1 cm at the rear end. Trawl depth was monitored during sampling by a Scanmar depth sensor, and nets were opened and closed on demand (acoustic transmission) from the ship. The trawl was towed at ~2 knots. The sampling design involved two modes of deployment. To assess vertical distributions, the trawl was towed obliquely from near-bottom waters to the surface, sampling five replicated (one replicate missing) depth intervals (400–300, 300–200, 200–100, 100–50 and 50–0 m) both day and night (Table I). To assess timing of evening vertical migration, the trawl was operated in horizontal mode, sampling five time intervals from 19 to 21 h with the trawl kept at 60 m in all tows.

Once on deck, ~10 individuals from each net were randomly picked for photography (see below for procedure). The remainder of the catch (or a subsample) was frozen in plastic bags at −20°C for later enumeration. In the lab, after ~3 months storage, shrimps were thawed and the length of the carapace was measured to the nearest 1.0 mm from the anterior tip of the rostrum to the mid-dorsal posterior end of the carapace.
The level of animal redness was assessed by digital photography. If applied with caution digital photography is a powerful method to investigate animal colouration (Vestheim and Kaartvedt, 2006; Stevens, 2007). The procedure is especially appropriate when investigating colouration in crustaceans where colour changes mediated by the presence of chromatophores and different distribution patterns of pigments rather than, or as well as, by changes in total pigment level (Ghidalia, 1985). In these situations, studies of extracted pigment concentrations will show no consistent depth-related trends (Fisher et al., 1952; Herring, 1973), while subjective assessments of their colour indicate that deep-living species are darker (Foxton, 1970). Digital photographing allows immediate shipboard assessment of animal colouration, eliminating effects on results from preservation procedures or time of storage.

The photographing procedure was strictly standardized. Immediately upon capture, the shrimps were gently narcotized by excess CO₂ produced by adding a small amount of Nyco fruktalt® (NaHCO₃, C₄H₆O₆, C₄H₄Na₂O₆·2H₂O, C₇H₅NO₃S) to the water. This treatment appeared not to affect the colouration and did not kill the animals. Thereafter, the animals were photographed with Nikon D200 camera (10.0 mega pixels) equipped with a Sigma 105 mm 1 : 2.8 D DG macro lens and a 58 mm Cokin circular polarization filter. The camera was set to sRGB (red–green–blue) mode, and all settings such as illumination, aperture, exposure, white balance and ISO speed ratings were kept constant. The camera was mounted on a closed dark box equipped with four cold light sources to assure standard background illumination. One by one, the animals were placed inside the box in a transparent, colourless dish filled with filtered seawater. The dish was positioned on a white background and kept at a constant distance from the camera. Every individual was photographed within 15 min after sampling. We trust this procedure assured measurements of “real” colouration, although chromatophore mediated colour changes may occur very rapidly in crustaceans (Boyle and McNamara, 2006; Auerswald et al., 2008).

Image analysis

Image analysis was performed in Aperio Technologies’ ImageScope version 7.3.36.1042 (free download) by running the Positive Pixel Count algorithm. The Positive Pixel Count algorithm quantifies the number of pixels in a given area which satisfy specific ranges of hues and saturations. Changing the default settings to a hue value of 0.04, a hue width of 0.40 and a colour saturation of 0.52 seemed to allow the red colour of the shrimps to be tracked very well. ImageScope allows for generating of mark-up images highlighting positive scored pixels so it is easy to check if the algorithm works as intended. The legs and antenna of the shrimp did not line up similarly in all photos and the area of the stomach was always dark red (see Fig. 1). Therefore, only the area behind the carapace without the legs was compared. To standardize the data set containing individuals of variable size, the number of positive scored pixels was divided by

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**Table 1: Exact time of the different vertical Sergestes tows**

| Series  | Depth  | Date          | Time start | Time stop |
|---------|--------|---------------|------------|-----------|
| Day 1a  | 300–400 m | 04 October 2006 | 12:42      | 12:55     |
| Day 1b  | 100–200 m | 05 October 2006 | 11:51      | 12:05     |
|         | 0–50 m  | 05 October 2006 | 12:12      | 12:20     |
| Day 2   | 300–400 m | 04 October 2006 | 14:10      | 14:23     |
|         | 200–300 m | 04 October 2006 | 14:25      | 14:39     |
|         | 100–200 m | 04 October 2006 | 15:30      | 15:41     |
|         | 50–100 m  | 04 October 2006 | 15:42      | 15:54     |
|         | 0–50 m  | 04 October 2006 | 15:56      | 16:05     |
| Night 1 | 300–400 m | 04 October 2006 | 20:30      | 20:42     |
|         | 200–300 m | 04 October 2006 | 20:43      | 20:56     |
|         | 100–200 m | 04 October 2006 | 21:47      | 21:59     |
|         | 50–100 m  | 04 October 2006 | 22:00      | 22:08     |
|         | 0–50 m  | 05 October 2006 | 21:12      | 21:20     |
| Night 2 | 300–400 m | 05 October 2006 | 22:04      | 22:18     |
|         | 200–300 m | 05 October 2006 | 22:19      | 22:29     |

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**Fig. 1.** Example of two shrimps of approximately same size displaying a variable amount of redness. Individual A was caught at 50–100 m depth during daytime (Day 1b), B was caught at 300–400 m depth at night-time (Night 2).
the squared length of carapace since this equalled the tail part area measured (data not shown).

In addition to assessing colouration, each photographed animal was subjectively inspected for the presence of food items in the digestive tract. If the digestive tract contained food, this made it appear opaque or coloured and clearly visible; if empty, the digestive tract was transparent in the pictures of these freshly collected animals.

Statistical analyses
Statistical analyses were performed in S-plus R 6.1 for Windows (Venables and Ripley, 2002) and STATISTICA (data analysis software system) version 8.0 StatSoft, Inc. Conditional density plots were made with standard Gaussian smoothing.

RESULTS
Temperature decreased from 14.5°C at the surface to 8.3°C at 75 m and was stable around 8.3–8.4°C all way down to the bottom. Salinity was 24.6 psu in the upper 2 m, increased rapidly to 30.6 psu at 4 m and stabilized around 35.0 from ~100 m. No differences in turbidity were detected with depth, but coloured dissolved organic matter was patchy and highest around 300 m.

Fluorescence (i.e. in vivo chlorophyll-a) maximum (0.7) was at 6 m from where it dropped to 0.1 at 18 m (Fig. 2).

Sergestes arcticus was captured throughout the whole water column, though very few individuals were caught in the upper strata during daytime (Fig. 3). Maximum abundance occurred between 200 and 300 m during the day and 0 and 50 m at night. Size measurements indicated the capture of three principal size classes,
with mean carapace lengths of 0.9, 1.6 and 1.9 cm (Fig 4). During daytime, individuals caught in the upper depth interval were significantly shorter than individuals found deeper for all depths except 0–50 m, but also here the mean length was shorter than below (Fig 5). Some shorter individuals were also caught at all depths during the day (Fig 5). At night, no trend of increasing carapace length with depth was found below 100 m (Fig 5). Sequential horizontal hauls at 60 m showed that small individuals appeared earlier in the upper layers than larger individuals (Fig 6).

Fewer individuals caught during the day (6%) had visible food items in their digestive tract compared with individuals caught at night (32%) ($\chi_2^2 = 13.01$, $P = 0.00$; Table II).

The individuals displayed a variable degree of redness (exemplified in Fig 1). Depth of capture was the most important factor explaining animal colouration, but also variation in the measured colouration increased with depth. During daytime, mean redness of individuals caught below 300 m was significantly higher than for individuals found above 200 m (Fig 7), and mean redness of those found below 200 m was significantly higher than for those found above 100 m (Fig 7). At night, only individuals found below 300 m had significantly higher mean redness than those caught higher in the water column (Fig 7).

Comparing all individuals caught at night with all those caught during the day did not reveal any overall differences in redness $F_{1,170} = 0.65$, $P = 0.42$. Nor was any overall difference in length of carapace between day

Fig. 4. Overall length distribution (length of carapace) of *Sergestes arcticus*, $N = 1206$.

Fig. 5. Length distribution (length of carapace) by depth during the day and at night-time of *Sergestes arcticus* calculated from all vertical tows. Mean lengths with 95% confidence intervals of the means and number of individuals measured are noted on top of each plot.
and night found, indicating that the same population was sampled day and night (mean day = 1.41 cm, mean night = 1.37 cm, $F_{1,1783} = 1.43, P = 0.23$). The WP2 samples were dominated by copepods and their numerical density was highest in the upper 50 m (6–10 times higher compared to all the succeeding depths) (Table III). *Acartia*, *Oithona*, *Paracalanus/Pseudocalanus* were the most abundant species. Other than copepods, a few chaetognaths, cnidarians and ostracods were also caught (Table III).

**DISCUSSION**

Smaller (indicating younger) individuals remained closer to the surface during day than larger (older) ones, in accordance with previous findings on segestids (e.g. Flock and Hopkins, 1992; Koukouras *et al.*, 2000). However, some small individuals were also found in the deepest depth strata during daytime. After dusk, smaller individuals appeared at shallow depths earlier than
larger ones, as expected from their generally shallower residence in the water column. De Robertis et al. (De Robertis et al., 2000) studying euphausiids also found that smaller bodied individuals arrived earlier at shallow depths, and also descended later than adults. We have no data from dawn to address whether larger bodied specimens left upper layers earlier than smaller ones, which would be expected for minimizing encounters with potential visual predators (Hays, 2003).

Ontogenic and size-dependent variations in DVM have generally been ascribed to large individuals being more conspicuous and therefore more susceptible to visual predators (e.g. Brooks and Dodson, 1965; Neill, 1992; Hays et al., 1994).

By photographing individual shrimps, we found that redness increased with depth of capture. This is in accordance with the predictions of Foxton (Foxton, 1970) and Herring and Roe (Herring and Roe, 1988) pointing out that by having large chromatophores and hence the ability to have a variable level of colouration, Sergestes should optimize its cryptic colouration to depth and time. Yet, such patterns have until now not been objectively documented for these shrimps. To be inconspicuous, Sergestes has internal photophores (light organs) functioning in countershading. Their downward-directed bioluminescence has a spectral emission (Widder et al., 1983), angular distribution (Latz and Case, 1982) and irradiance (Warner et al., 1979), all consistent with a camouflage function. The ability of the shrimp to alter body colouration provides yet another way to adapt to the prevailing light regime.

Variance in redness also increased with depth. Furthermore, during daytime, individuals caught above 100 m were significantly less red than those found below 200 m. However, at night-time only individuals found below 300 m had significantly higher mean redness than those caught higher in the water column. One possible explanation of why several low-coloured individuals were found in mid-waters at night is that these individuals had just arrived from a visit to upper layers and had not yet adjusted their colouration to the light regime at the depth of capture. Another possibility could be that they were late migrants or even or return migrants from an earlier feeding during this night, which were pre-adjusted to light conditions in the upper waters. This could be tested in future studies with more comprehensive analyses of stomach contents.

Very few individuals captured during the day had visible gut contents, while this proportion increased markedly already early at night. That feeding mainly seemed to take place at night has also been reported for other vertically migrating species of Sergestes [S. lucens (Omori and Gluck, 1979), S. similis (Judkins and Fleminger, 1972)]. The WP2 net samples also showed that number of copepods (i.e. potential prey) was by far highest in the upper 50 m. We only have daytime zooplankton samples, and night-time samples might have shown an even higher proportion of prey in upper waters. We believe that the upward vertical migrations in Sergestes most likely were hunger-driven. The hunger/satiation hypothesis (see Pearre, 2003) predicts that animals should make short intermittent forays into surface waters where there is high food concentration, but also an increased risk of predation, and then return to intermediate depths to reduce risks they digest. Our results are consistent with this prediction.

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