T.M. Frank · E.A. Widder

Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton

Abstract The daytime vertical distribution of several species of crustaceans, gelatinous zooplankton, and fish were monitored in situ simultaneously with measurements of downwelling irradiance in Oceanographer Canyon in July 1999. During this submersible-based research cruise, an influx of turbid water significantly decreased downwelling irradiance and had a substantial impact on the depth distributions of a number of organisms. Several species of crustaceans, (*Thysanoessa gregaria* and *Sergestes arcticus*) and gelatinous zooplankton (*Salpa aspera* and *Salpa fusiformis*) ascended over 100 m in the water column during the influx and returned to their pre-influx depths once the influx had ceased. In situ light measurements demonstrated that each of these species was associated with the same irradiance levels during the influx as they were under pre- and post-influx conditions. By contrast, a statistically significant change in temperature, salinity, and oxygen concentrations measured post-influx had no apparent impact on the depth distributions. These results indicate that these species were adjusting their depth distributions to remain within a range of preferred irradiances. Electronic supplementary material to this paper can be obtained by using the Springer LINK server located at http://dx.doi.org/10.1007/s002270020788

Introduction

Vertical migration is one of the most widespread animal behavior patterns in the world and has been studied intensively for almost 100 years. Considerable evidence has been accumulating in the shallow water (< 100 m) realm that predator avoidance is the ultimate (i.e. adaptive) cause of vertical migrations (see Lampert 1993 and DeMeester et al. 1999 for reviews), and there is no reason to assume that this is not also the adaptive value of vertical migrations in the mesopelagic environment. However, there is no consensus on the proximate factors controlling vertical migrations. When vertical migrations are occurring on a daily basis, it is generally accepted that light is the primary proximate cue that controls the timing of the migrations, since most vertical migrations occur at sunset and sunrise (for reviews, see Forward 1988; Haney 1988; Ringelberg 1995). However, there are several aspects of the environmental light field that could serve as cues to initiate these migrations.

One hypothesis that has received considerable attention is the preferendum hypothesis, which suggests that vertically migrating organisms remain within a preferred light zone, or isolume, and migrate up as the light intensity decreases at sunset and back down as intensity increases at sunrise (Ewald 1910; Michael 1911). Studies on shallow water species in the field and laboratory indicate that in general, zooplankton species are not following an isolume (Swift and Forward 1988; Wagner-Dobler 1990) but, rather, are responding to the rate of change in light intensity as the trigger for their migrations (Forward 1988; Forward and Hettler 1992; Van Gool and Ringelberg 1997). However, results of field studies in the mesopelagic environment have been ambiguous and confusing, as discussed in Frank and Widder (1997). A drawback of these studies is that the number and identity of the different species involved were unknown, and the contradictory results could simply be due to the fact that different species were involved. Roe and his colleagues (Roe 1983, 1984a, b; Roe et al. 1984), attempted to correlate downwelling light levels with movements of migrating fish and shrimp by quantifying net-collected samples. A major problem with this methodology is that there was no way of ensuring that the light meter attached to the net was at

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T.M. Frank (✉) · E.A. Widder
Harbor Branch Oceanographic Institution,
5600 U.S. 1 N, Ft. Pierce, FL 34946, USA

E-mail: frank@hboi.edu
Tel.: +1-561-4652400 ext. 311
Fax: +1-561-4680757

the same angle for each trawl, a critical parameter when attempting to measure changes in downwelling light. In addition, a major drawback of all the earlier studies is that the spectral responsivity of the light meters used did not match that of the migrators. Since the preferendum hypothesis refers to a preferred subjective light level, the isolume for an organism will depend on the spectral sensitivity of its eyes. Photometers fitted with narrow-band interference filters do not account for the impact of changing spectral distribution with depth and therefore may not accurately measure the speed of an isolume, especially at shallower depths (Widder and Frank 2001).

If vertical migrators are in fact trying to remain at a preferred light level, then it follows that the daytime depth distributions for these migrators should vary with changes in either surface irradiance or water transparency. However, data from studies of daytime movement patterns in the mesopelagic realm are also inconclusive. Several studies have indicated that the daytime depths of occurrence of some mesopelagic fish species are linked to water transparency (Woodhead 1966; Dickson 1972; Isaacs et al. 1974; Kampa 1976). However, these studies relied primarily on the study of sonic scattering layers (SSLs), in which species distributions had not been established. In addition, several authors (Blaxter 1975; Heath et al. 1988; Neilson and Perry 1990) have observed that most of these studies relied on qualitative estimates of the depth distributions of the populations being studied and, in some cases, suffer from the lack of in situ measurements of the variables in question. A more recent study by Buskey et al. (1989) demonstrated unequivocally that the mesopelagic copepod *Pleuromamma* has a deeper daytime depth distribution in the clearer waters of the southern Sargasso Sea than in the more turbid waters to the north, and Kaartvedt et al. (1996) found a similar distribution for *Maurolicus muelleri*, a mesopelagic fish. In addition, scattering layers presumably containing primarily *M. muelleri* moved up or down in response to short-time fluctuations in light intensity (Giske et al. 1990; Baliño and Aksnes 1993; Rasmussen and Giske 1994). Conversely, Onsrud and Kaartvedt (1998) found that the daytime depth of the krill scattering layer was fairly constant even though estimated light intensities at the leading (shallowest) edge of the layer differed by two orders of magnitude over the course of their study. These studies, however, were based on the movements of SSLs, and it is difficult to draw solid conclusions from studies of SSLs, even when coupled with periodic trawling, as Hopkins et al. (1978) found that the SSL in Balsfjorden was a dynamic assemblage showing diurnal changes in species composition. Based on trawled samples, *M. norvegica* was at times well represented in the SSL but at other times was absent from it. Other studies have found similar complexities in zooplankton SSLs (Hopkins and Evans 1979; Pearre 1979; Witek et al. 1981; Sameoto 1983; Shulenberger et al. 1984).

On an expedition to Oceanographer Canyon (at the south edge of Georges Bank) in July 1999, a serendipitous influx of turbid water in the middle of the expedition resulted in a prolonged period of decreased irradiance. Using the "Johnson-Sea-Link" submersible, we were able to measure animal distribution patterns simultaneously with downwelling irradiance before, during, and after the turbid influx, providing, for the first time, in situ data on the effect of changes in irradiance on animal distribution patterns.

Materials and methods

The "Johnson-Sea-Link" submersible was used as a platform from which to conduct in situ measurements of animal distributions simultaneously with measurements of downwelling irradiance in Oceanographer Canyon (68°08′N, 40°19′W) during July 1999. Oceanographer Canyon was chosen as the study site because it is an area of high abundance and low diversity with respect to the larger zooplankton species, allowing for submersible-based identification to the genus level, and in some cases to the species level, of the larger migrating organisms. Animal distribution patterns were quantified via visual transects, and irradiance measurements were made before and after each transect.

Visual transects

Transects were conducted as described in Frank and Widder (1997). Briefly, transects were run for 4 min at a forward speed of 0.6 knots. Organisms entering a 2.65 m^2 rectangular area were identified and recorded to tape by the scientist (TMF or EAW) seated in the front chamber of the "Johnson-Sea-Link" submersible, which is a 152-cm Plexiglas sphere. Transects were conducted every 50–100 m, from 100 m to 800 m depth, between 10:00 and 13:30 EST. Organisms were periodically caught with samplers on the front of the submersible (euphausiid crustaceans, salps, and siphonophores) or with a trawl net at night (euphausiid and sergestid crustaceans and fish) to verify species identifications made during transects. These two different collecting techniques were necessary because sergestid crustaceans and fish could not be collected with the submersible, and gelatinous zooplankton are destroyed when collected by trawl nets, making identification to species difficult. Trawling was only carried out at night, when the submersible was out of the water, and trawls were conducted from 100 m to 700 m depth. Several dives were also made between 18:30 and 22:00, to track the vertical migrations of these species at sunset. Due to weather constraints, not enough dives were made to obtain sufficient data for statistical analysis. Therefore, all the data presented here were collected on visual transects conducted on the day dives.

Measurements of environmental parameters

Light measurements were made with the Low Light Autoradiometer (LoLAR), a PMT-based autocalibrating radiometer that was mounted on the submersible (Widder et al. 1992; Frank and Widder 1997). One slot of the LoLAR's two-position filter wheel was fitted with a 480-nm interference filter (full-width half-maximum intensity = 10 nm). The second slot was fitted with a "shrimp filter" that was selected such that the detector/filter combination would result in a weighted responsivity that was comparable to that of a vertically migrating mesopelagic shrimp (Widder and Frank 2001). Measurements were made with both filters throughout this investigation. Although the shrimp filter provides a better estimate of the true irradiance available to a photoreceptor, there is no way to calibrate this filter to give a true estimate of the downwelling irradiance. Rather, values would have to be presented in "shrimp lux" units, similar to mylux units described by Gal et al. (1999), which are currently not useful for comparison with other studies.

Data analysis indicated that there was no significant difference in our conclusions whether the analysis was done using irradiance measurements taken with the 480-nm filter or with the "shrimp filter," since all of the daytime measurements reported here were made at depths where the spectral distribution changes very little with depth. Therefore, all irradiance measurements are reported in units of photons cm^{-2} s^{-1} nm^{-1} at 480 nm. In situ downwelling irradiance measurements were made to a depth of 500 m during pre-influx and post-influx conditions, and down to 400 m during the turbid water influx. Values at deeper depths for each dive were calculated using the diffuse attenuation coefficient, k_{480}, that was calculated from the deepest measurements taken on that dive.

Salinity (‰), temperature (°C), and oxygen saturation (milliliters per liter) measurements were made on each submersible dive with a Seabird Model 25 CTD mounted on the submersible. Fluorescence (V) was measured with a SeaTech Model FLF-026 fluorometer mounted on the submersible.

Data analysis

Environmental data

Mean data (irradiance, temperature, salinity, oxygen saturation, and fluorescence) from before the influx, during the influx, and after the influx were analyzed with the paired two-sample t-test for means (Zar 1974).

Animal data

Due to the patchy nature of the ocean environment (cf. Table 1), transect data for each species enumerated on a dive were normalized to the peak abundance for that species on that dive (Frank and Widder 1997). If several transects were conducted at one depth or irradiance range on a dive, data from these replicates were averaged so each dive contributed one data point to each depth or irradiance range in the final analysis. This averaging was necessary because equal numbers of replicates could not be conducted on each dive. The averaged data were analyzed with a single-factor ANOVA. If statistical significance was established with this test, the Newman–Keuls multiple range test for unequal sample sizes was used to determine where the statistical significance (at the 0.05 level) occurred among the sample means (Zar 1974).

Depths were divided into 125-m bins, the smallest range at which there was a large enough sample size for statistical significance. Irradiances were divided into 2-log-unit bins for the same reason.

Results

Environmental data

During this cruise, an influx of cold water reduced sea surface temperatures to such an extent that the change was visible on NOAA satellite images (Fig. 1 – also available as electronic supplementary material). Conductivity-temperature-depth (CTD) measurements indicated that surface temperatures dropped by 2°C (Table 1). This cold water influx was also quite turbid (Fig. 2). Based on surface temperature (Table 1) and downwelling irradiance (Fig. 2), data from 11 July through 15 July were grouped together as "pre-influx" data. July 16 was a transition day, and the irradiance and temperature were dropping. Due to inclement weather, no dive was conducted on 17 July. July 18–20 were days during which irradiance and temperature measurements were at their lowest, and data from these days were grouped together as "influx" data. Irradiance and temperature data from 21 July indicated that this was another transition day, in which conditions were starting to return to pre-influx values. Data from 22–23 July indicated that downwelling irradiance and temperature had returned to pre-influx values, and these data were grouped together as "post-influx" data. Because the environmental data showed the greatest variation in surface waters, and all the species of interest in the study were found below 150 m, the data are graphed in two sets – data measured in the upper 150 m of water, and data measured below 150 m.

Temperature

There was a substantial decrease in temperature in the top 50 m of water during the influx, with mean surface temperatures almost 2° lower than under pre- and post-influx conditions (Fig. 3A; Table 1). However, there is no significant difference in temperatures measured under pre-influx conditions and during the influx at depths greater than 150 m (Fig. 4A). Temperatures at depths greater than 150 m under pre-influx conditions and during the influx are both significantly lower than temperatures measured under post-influx conditions.

Salinity

Salinity in the upper 100 m of water was highly variable (Fig. 3B), but below 150 m there is no significant difference in salinities measured under pre-influx conditions or during the influx (Fig. 4B). The salinities measured under post-influx conditions are significantly higher than those measured both under pre-influx conditions and during the influx.

Oxygen saturation

Oxygen saturation in surface waters was also highly variable (Fig. 3C), but there is no significant difference in oxygen saturation measured below 150 m depth under pre-influx conditions and during the influx (Fig. 4C). Oxygen saturation measured under post-influx conditions is significantly lower than both during the influx and under pre-influx conditions (Fig. 4C).

Fluorescence

There was a significant subsurface fluorescence maximum under all three conditions, as is characteristic of the seasonally stratified water in this area (O'Reilly et al. 1987), with the maximum ranging from 40 m under pre-influx conditions to 60 m under post-influx conditions (Fig. 3D). However, below 150 m, data measured during the influx are not significantly different from data

Table 1. Maximum number of organisms per cubic meter quantified on each dive

Date	Temp (°C) at 5 m	Small euphausiids	Large euphausiids	*Sergestes arcticus*	*Nanomia cara*	Myctophids	Salps
Pre-influx							
11 July 1999	22.8	1.224	0.056	0.025	0.066	0.051	0.209
12 July 1999	23.6	0.296	0.015	0.056	0.184	0.020	0.153
15 July 1999	24.1	NA[a]	NA[a]	0.158	0.224	0.031	0.178
Transition							
16 July 1999	23.8	0.484	0.158	0.075	0.280	0.102	0.265
Influx							
18 July 1999	21.6	0.087	0.031	0.496	0.454	0.300	0.165
19 July 1999	21.4	0.153	0.418	0.235	0.255	0.474	0.112
20 July 1999	21.6	0.372	0.071	0.133	0.372	0.204	0.235
Transition							
21 July 1999	22.6	0.046	0.076	0.138	0.678	0.263	0.214
Post-influx							
22 July 1999	23.5	0.116	0.086	0.135	0.661	0.135	0.098
23 July 1999	23.4	0.066	0.336	0.041	0.127	0.031	0.005

[a] Shallowest transect depth was 500 m – dive called up early due to inclement weather

measured under post-influx conditions (Fig. 4D). Data measured under pre-influx conditions are significantly different from data measured both during the influx and under post-influx conditions.

Downwelling irradiance

There was a decrease in downwelling irradiance during the influx below 150 m, and an increase in downwelling irradiance once the influx had ceased. The downwelling irradiance during the influx is significantly lower than irradiance measured during either pre- or post-influx conditions (Fig. 4E). Downwelling irradiance measured during the pre-influx period is not significantly different from that measured during the post-influx period.

Daytime depth distributions

The following organisms were quantified during the visual transects:

- Euphausiids. During the transects, there was a noticeable difference in the size of the euphausiids being quantified, and these broke into two distinct size classes – small and medium/large. Although small juveniles of both *Nematoscelis megalops* and *Meganyctiphanes norvegica* were abundant in the trawl net, samples collected during the transects, which are substantially more discrete than net trawls, indicated that the vast majority (90%) of the small euphausiids being quantified during the transects were *Thysanoessa gregaria,* whereas all the medium to large euphausiids were *N. megalops* and *M. norvegica*. The two species of larger euphausiids could not be distinguished from each other on transects but were easily separated from the small euphausiids. For this reason, the distribution patterns of the euphausiids are presented separately for large (*N. megalops* and *M. norvegica*) and small (*T. gregaria*) euphausiids.
- Sergestids. *Sergestes arcticus* is the only species of *Sergestes* found in Oceanographer Canyon. Several species of all-red *Sergia* were also present but were too rare for statistical analysis.
- Salps. Two species of salps were present on this cruise – *Salpa aspera* and *S. fusiformis*. They could not be distinguished from each other on transects and are therefore grouped together.
- Siphonophores. Several species of siphonophores were present, but only one, *Nanomia cara*, was present in any abundance, and it was easily distinguished from the other species present.
- Myctophid fish. Myctophids could not be caught during transects, but trawls were conducted at the depths at which myctophids were quantified on submersible dives. The trawl data indicated that *Benthosema glaciale* was present in great abundance, whereas *Lampadena* sp. was very rare. However, because myctophid species could not be distinguished from each other during transects, they are grouped together as myctophids.

Data collected on the three dives before the influx were grouped with data collected on the two dives after the influx had ceased and are referred to as "normal" data. Data taken from three dives during the influx were grouped and are referred to as "influx" data.

The depth distribution of the small euphausiids, sergestids, and salps changed significantly during the influx, with significant portions of each group migrating approximately 125 m into shallower water (Fig. 5A–C). The myctophids did not migrate to shallower water during the influx (Fig. 5D). Their distribution was quite diffuse and covered the same depth ranges under normal and influx conditions, with the shallowest individuals as well as statistically significant portions of the community present between 375 and 500 m. In addition, during influx conditions, a statistically significant portion of the community was actually found at deeper depths than under normal conditions.

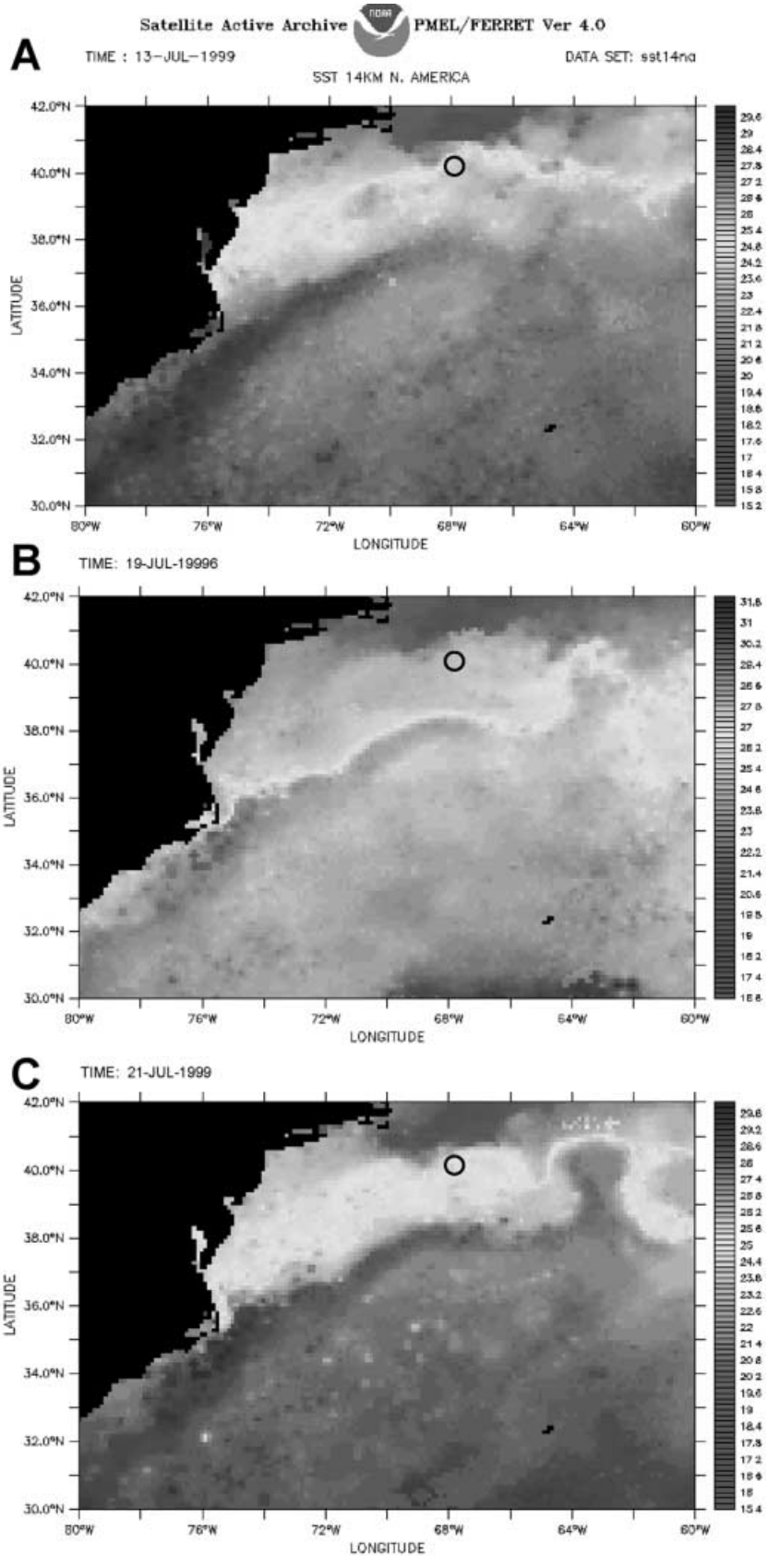

Fig. 1. Satellite images of sea surface temperatures (from NOAA Satellite Active Archive) before the influx (**A**), during the influx (**B**), and after the influx ended (**C**). *Open circles* designate study site. Also available as electronic supplementary material

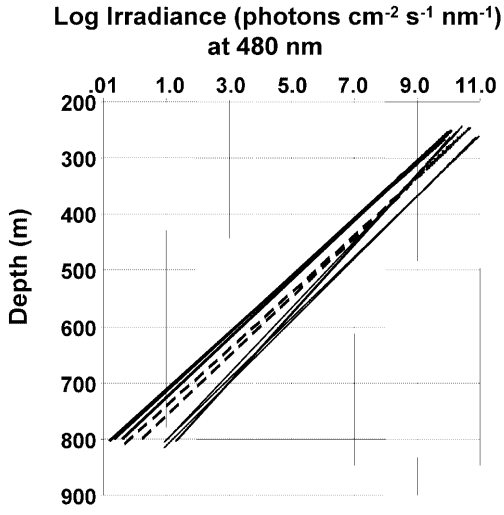

Fig. 2. Downwelling irradiance versus depth in Oceanographer Canyon. The *lines* shown are linear regression fits to the data and are from five dives before and after the influx (*thin solid line*), two dives during transition periods (*dashed line*), and three dives during the influx (*thick solid line*). In situ data were taken down to 500 m under normal conditions, and down to 400 m during the influx. At deeper depths, irradiance was calculated according to the formula: $E_{z_2} = E_{z_1} e^{-k(z_1 - z_2)}$ where E is irradiance in photons cm^{-2} s^{-1} nm^{-1}, z_1 is depth 1, z_2 is depth 2, and k is the diffuse attenuation coefficient at 480 nm, calculated from the deepest in situ irradiance measurements on that dive

For the community of large euphausiids, the migration pattern is not so clear (Fig. 5E). Statistically significant portions of the community were found at the same depth ranges under normal conditions and during the influx. However, individuals were quantified down to 750 m under normal conditions, whereas none were found deeper than 500 m during the influx. In addition, there were individuals between 250 and 375 m during the influx, whereas none were seen at this shallow depth range under normal conditions. The data for *N. cara* are similarly ambiguous (Fig. 5F). Under both normal and influx conditions, statistically significant portions of the population were present between 626 and 750 m. The portion present between 500 and 625 m is statistically significant under influx conditions, whereas under normal conditions, it is not, even though a substantial number of individuals were present at this depth. In addition, the distribution of both the shallowest and deepest individuals present were the same under normal and influx conditions.

Distribution versus environmental parameters

A variety of exogenous factors are known to affect the depth distributions and vertical migrations of organisms (Forward 1988), but only four of these might have been affected by the influx – temperature, salinity, oxygen, and light. While there were substantial changes in some of these factors in surface waters, all the species in this study had daytime depths of below 150 m and would therefore only be affected by changes in these factors below this depth. There are no significant differences in temperature, salinity, and oxygen saturation data measured before the influx and those measured during the influx at depths below 150 m, yet during this time, the depth distribution of several of the species in this study changed by over 100 m.

Fluorescence can be taken as an indication of the relative levels of chlorophyll in the water column in this area, as there is a significant linear relationship between measured fluorescence and extracted chlorophyll (Mountain and Taylor 1996). While changes in chlorophyll levels may not directly affect the depth distributions of the species in the study, it may affect the depth distributions of some of their prey, such as copepods (Huntley and Brooks 1982), and therefore may have an effect on the daytime feeding depths of the species in the study, as well. However, while the depth of the fluorescence maximum shifted between pre-influx, post-influx, and influx conditions, this occurred at least 150 m above the depth at which any of the relevant species were present during the day, indicating that even if their prey congregated in a chlorophyll maximum, the species of interest were not following their prey into shallower waters. In addition, below 150 m, the fluorescence data taken during the influx and under post-influx conditions are not significantly different. The only factor during the influx that was significantly different from data quantified under *both* pre- and post-influx conditions at depths below 150 m was irradiance.

When analyzed with respect to downwelling irradiance, there was no significant difference in the distribution of the small euphausiids under normal conditions and during the influx (Fig. 6A). Significant portions of the population were associated with irradiance levels of 10^6–10^9 cm^{-2} s^{-1} nm^{-1} under both conditions. The same pattern is true for *Sergestes arcticus* (Fig. 6B) and the salps (Fig. 6C) – statistically significant portions of each group were present at the same irradiance levels under normal conditions and during the influx. For both the myctophids (Fig. 6D) and *N. cara* (Fig. 6F), a significant portion of each group was associated with brighter light intensities under normal conditions than during the influx. For the myctophids, statistical significance is found at 10^6–10^7 photons cm^{-2} s^{-1} nm^{-1} under normal conditions, whereas during the influx, the brightest irradiance at which significant numbers were found was 10^4–10^5 photons cm^{-2} s^{-1} nm^{-1}. For *Nanomia,* significant numbers were associated with an irradiance level of 10^4–10^5 photons cm^{-2} s^{-1} nm^{-1} under normal conditions, while the brightest irradiance at which significant numbers of individuals were present during the influx was 10^2–10^3 photons cm^{-2} s^{-1} nm^{-1}. There were not enough individuals associated with any light range to get statistical significance for the large euphausiids (Fig. 6E). Looking at the overall distribution, it appears that most of the large euphausiid community occupied the same range of intensities under normal and influx conditions, with a small portion of the community found at lower light levels under normal conditions than during the influx.

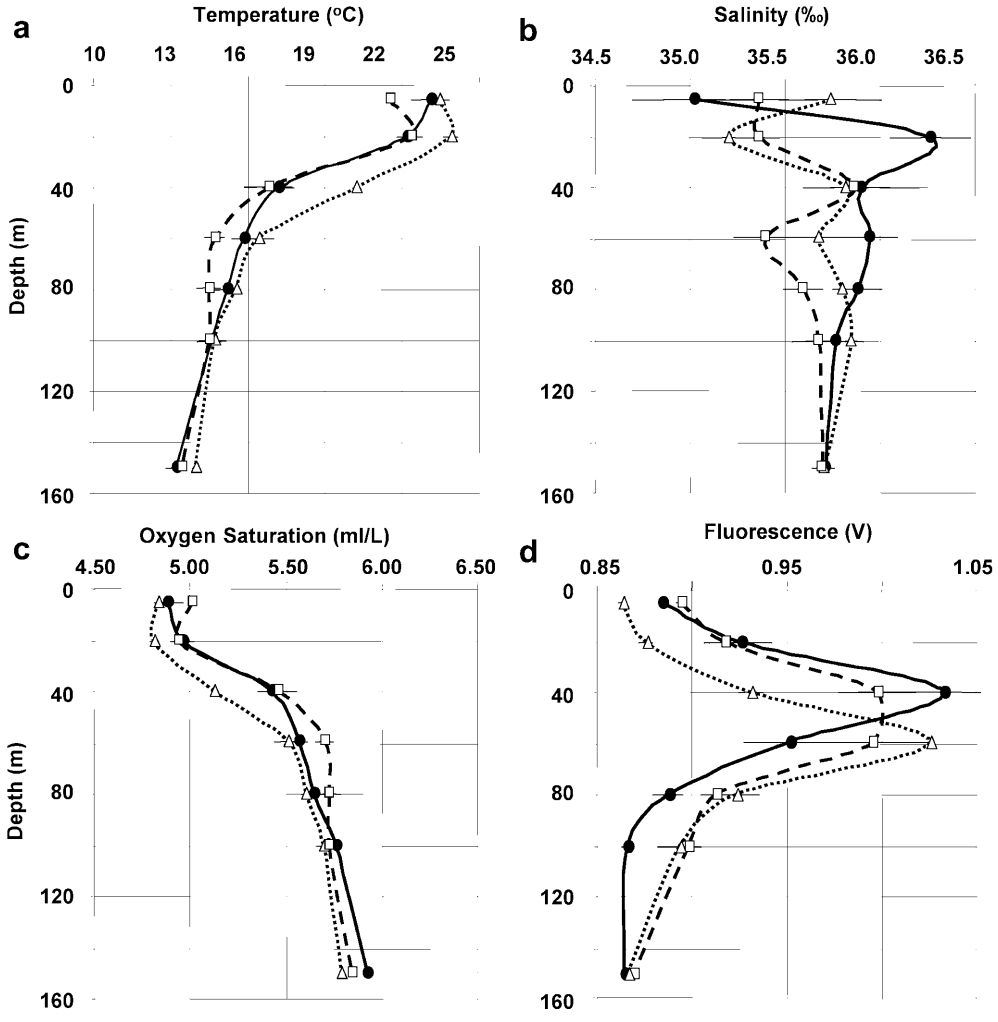

Fig. 3A–D. Environmental parameters versus depth from 0 to 150 m in Oceanographer Canyon for pre-influx (*circles*), influx (*squares*), and post-influx (*triangles*) conditions. *Bars* indicate standard errors. **A** Temperature versus depth. **B** Salinity versus depth. **C** Oxygen saturation versus depth. **D** Fluorescence versus depth

Discussion

There are two main sources of water on Georges Bank – cold fresh Scotian Shelf surface water and the deep inflow of warm saline slope water (Bigelow 1927). The influx of water observed on this cruise was apparently Scotian Shelf water, as it resulted in a noticeable decrease in both surface temperature and salinity (Fig. 3A, B). The water mass was also very turbid, as evidenced by the decrease in downwelling irradiance during the influx, and had a significant effect on the daytime depth distributions of the small euphausiids, the sergestid *Sergestes arcticus*, and the salp species. For these species, statistically significant portions of the populations are found at shallower depths during the influx than before or after the influx, and it appears that the entire population of each species ascended approximately 125 m to shallower water. For the large euphausiids, the statistically significant portion of the community was at the same depth before and during the influx. However, the deepest individuals were found down to 750 m before and after the influx, whereas during the influx, no individuals were seen deeper than 500 m. In addition, under normal conditions, no individuals were seen shallower than 375 m, whereas during the influx, individuals were present at 250 m. Thus, although there is no statistically significant difference in the position of the community under normal conditions and during the influx, a trend toward shallower water by the community as a whole is apparent.

The siphonophore *Nanomia cara* and the myctophids were seemingly unaffected by the influx, with both groups maintaining approximately the same depth distributions under both conditions. A significant portion of the *N. cara* population was found between 500 and 625 m during the influx, while the numbers found at this depth under normal conditions were not statistically significant, although this is the depth range at which the second highest concentration of *Nanomia* was present under normal conditions. Because the rest of the population had essentially the same depth distribution, that is, shallowest and deepest individuals were seen at the same depths under normal conditions and during the influx, it appears that the overall distribution of *Nanomia* did not change during the influx. With the myctophids, the situation is clearer. Statistically significant portions of the community had the same minimum

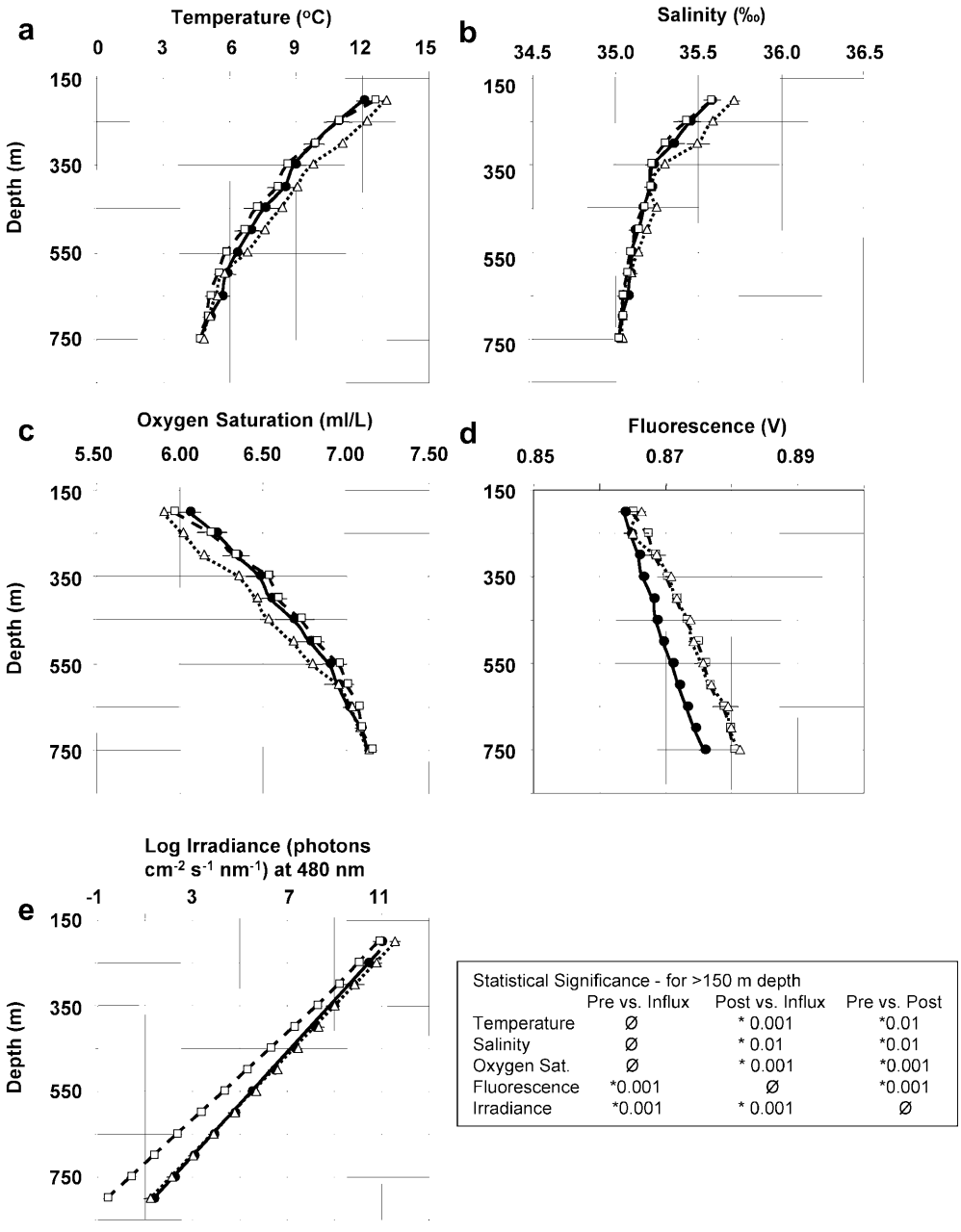

Fig. 4A–E. Environmental parameters versus depth from 200 to 750 m in Oceanographer Canyon for pre-influx (*circles*), influx (*squares*), and post-influx (*triangles*) conditions. *Bars* indicate standard errors. **A** Temperature versus depth. **B** Salinity versus depth. **C** Oxygen saturation versus depth. **D** Fluorescence versus depth. The temperature, salinity, and oxygen saturation data measured during pre-influx conditions are not significantly different from those measured during the influx, whereas data measured during post-influx conditions are significantly different from both pre-influx and influx data. The fluorescence data measured under pre-influx conditions are significantly lower than data measured during the influx or under post-influx conditions. Data measured during post-influx conditions are not significantly different from those measured during the influx. **E** Downwelling irradiance versus depth. *Lines* drawn through the data are linear regression fits. Irradiance during the influx is significantly lower than irradiance measured under pre- or post-influx conditions, whereas pre-influx and post-influx irradiance values are not significantly different from each other

depth under normal conditions and during the influx, and some members of the community were actually significantly deeper during the influx than under normal conditions.

The staggered vertical distribution of the various species in this study is similar to what has been found in other regions where the same or similar species of organisms co-occur. In the 400-m-deep Masfjorden, western Norway, the populations of *Meganyctiphanes norvegica* and *Sergestes arcticus* overlapped to some extent, but the population maximum of *S. arcticus* was deeper than that of *M. norvegica* (Kaartvedt et al. 1988). In addition, as in Oceanographer Canyon, the distribution of the myctophid species overlapped the peaks of both the euphausiid and sergestid populations. Vertical partitioning of smaller species or smaller individuals of the same species to shallower water, and larger species or larger individuals of the same species to deeper water, has been demonstrated for several species of euphausiids (Andersen and Sardou 1992; Kaartvedt et al. 1996) and copepods (Buskey et al. 1989). Size partitioning within a species has been reported for copepods (Buskey et al. 1989; Hays et al. 1994), the pasiphaeid *Pasiphaea multidentata* (Matthews and Pinnoi 1973), the sergestid *S. arcticus* (Roe 1984a), the euphausiid *Euphausia pacifica* (De Robertis et al. 2000), and several species of teleost – *Argyropelecus hemigymnus* (Roe 1983) and *Maurolicus muelleri* (Giske et al. 1990). The staggered daytime depth distributions for the crustaceans in our study seems to fit this pattern of increasing size with

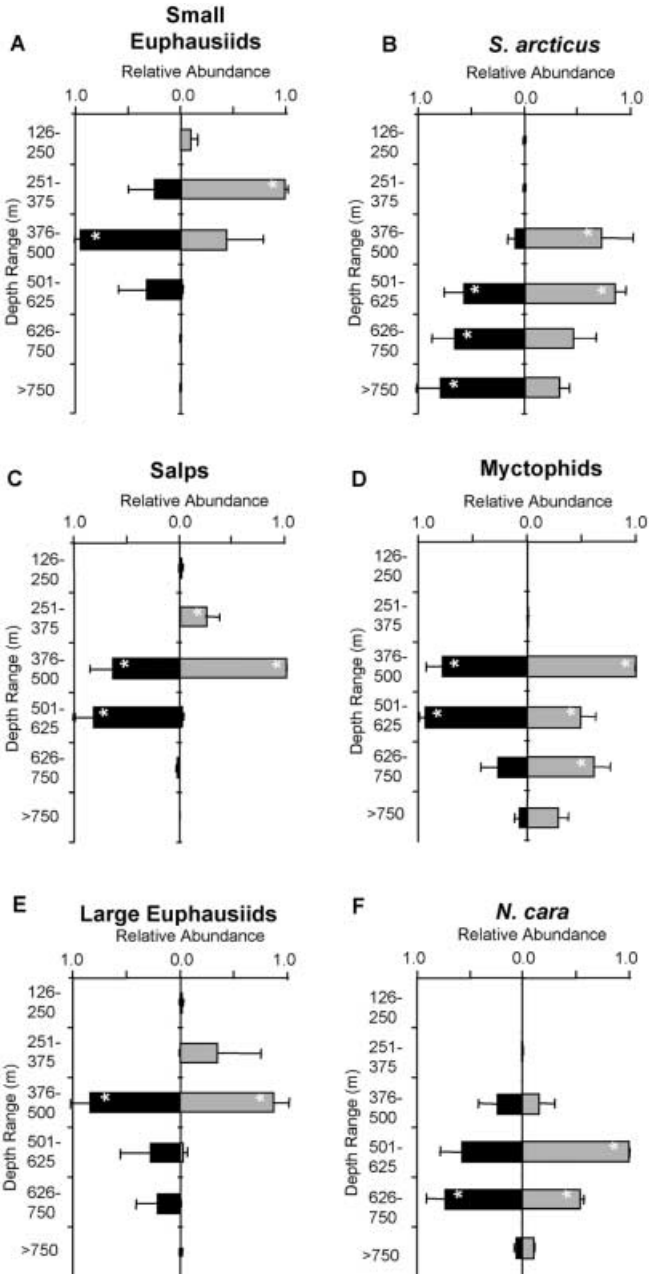

Fig. 5A–F. Relative daytime abundance versus depth. *Black bars* indicate data taken under normal conditions (both before and after the influx). *Gray bars* indicate data taken during the influx. *Asterisks* indicate data that are statistically significant at the 0.05 level, utilizing the Newman–Keuls multiple range test for unequal sample sizes (Zar 1974). *Error bars* represent standard errors. Abundances have been normalized as described under Materials and methods. **A** Daytime depth distribution of the small euphausiids *Thysanoessa gregaria*. **B** Daytime distribution of the sergestid *Sergestes arcticus*. **C** Daytime distribution of the salp species *Salpa fusiformis* and *S. aspera*. **D** Daytime distribution of the myctophids *Benthosema glaciale* and *Lampydena* sp. **E** Daytime distribution of the large euphausiids *Nematoscelis megalops* and *Meganyctiphanes norvegica*. **F** Daytime distribution of the siphonophore *Nanomia cara*

depth. The small euphausiids had the shallowest depth distribution of all the species studied, followed by the large euphausiids, followed by the sergestids, adult specimens of which were larger than the largest euphausiids in this area. Based on studies of mesopelagic fish, Giske et al. (1990) suggested that juveniles or smaller species have shallower distributions than adults or larger species because they are less visible in more illuminated waters, and this pattern appears to be present in zooplankton as well.

Analyzing the species' distributions with respect to downwelling irradiance produced some interesting results. For the species that made a significant migration (~125 m) to shallower water during the influx (*Thysanoessa gregaria*, *Sergestes arcticus*, *Salpa fusiformis* and *S. aspera*), there were no differences in their distributions with respect to downwelling irradiance under normal conditions and during the influx. Statistically significant numbers of all four species were associated with the same irradiance levels under normal conditions and during the influx. These data suggest that these species were adjusting their daytime depth distribution to remain within a preferred range of light intensities. For *Nanomia cara* and the myctophids, which did not move to shallower water during the influx, statistically significant portions of both populations were found at dimmer light levels during the influx than under normal conditions. This can be explained by the fact that these species maintained their depth distributions during the influx of turbid water, which significantly decreased downwelling irradiance at their normal daytime depths.

In their 1996 study of the distribution of fish and euphausiids across the shelf off northern Norway, Kaartvedt et al. (1996) found that, at one station, the vertical distributions of the upper (interpreted as fish) and middle (interpreted as euphausiids) SSLs were approximately 100 m shallower than at other locations in the study and were accompanied by a rise in the demersal fish layer. This change in vertical distribution was associated with a front in which surface salinity and temperature values decreased and chlorophyll a values and light extinction values increased. However, it is difficult to determine whether the ascent of the euphausiids was a function of the decrease in downwelling irradiance, or due to the ascent of demersal planktivorous fish, which might have been responding to the decrease in downwelling irradiance. In our study, the only fish present in any quantity, based on both submersible observations and midwater trawls, was the myctophid *Benthosema glaciale*. The primary food of *B. glaciale* is copepods (Sameoto 1988; Gjøsæter 1973), but they do prey on euphausiids as well, primarily *Thysanoessa* spp. and the smaller *Meganyctiphanes norvegica* (Gjøsæter 1973). However, *B. glaciale* did not migrate to shallower water during the influx, so the ascent of the euphausiids appears to be a direct response to the decrease in downwelling irradiance.

Several studies have used SSL together with trawling studies to monitor the vertical distribution of *M. norvegica* during the day. In Oslofjord, Norway, *M. norvegica* lived below 70 m during the day (Onsrud and Kaartvedt 1998), while in fjords along the western

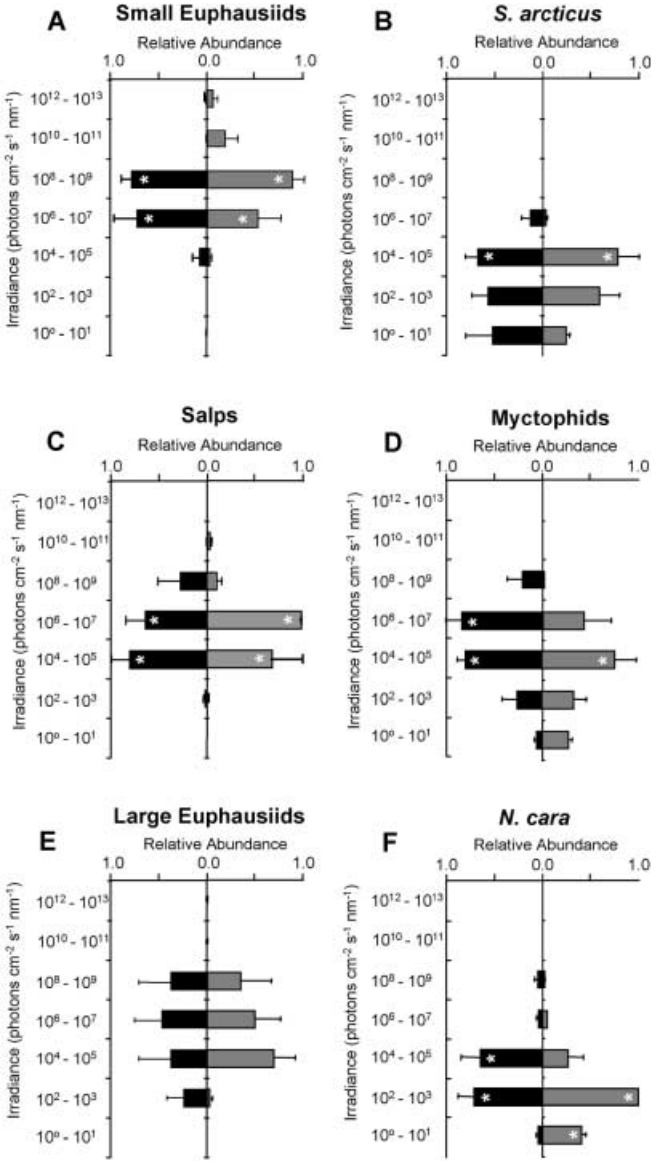

Fig. 6A–F. Relative daytime abundance versus downwelling irradiance. Downwelling irradiance is plotted from highest to lowest. *Black bars* indicate data taken under normal conditions (both before and after the influx). *Gray bars* indicate data taken during the influx. *Asterisks* indicate data that are statistically significant at the 0.05 level, utilizing the Newman–Keuls multiple range test for unequal sample sizes (Zar 1974). *Error bars* indicate standard errors. Abundances have been normalized as described under Materials and methods. **A** Daytime irradiance distribution of small euphausiids *Thysanoessa gregaria*. **B** Daytime irradiance distribution of the sergestid *Sergestes arcticus*. **C** Daytime irradiance distribution of the salps *Salpa fusiformis* and *S. aspera*. **D** Daytime irradiance distribution for the myctophids *Benthosema glaciale* and *Lampydena* sp. **E** Daytime irradiance distribution for the large euphausiids *Meganyctiphanes norvegica* and *Nematoscelis megalops*. **F** Daytime irradiance distribution for the siphonophore *Nanomia cara*

Norwegian coast, they lived primarily below 100 m (Evans and Hopkins 1981; Giske et al. 1990; Baliño and Aksnes 1993). Onsrud and Kaartvedt (1998) suggest this is because the downwelling light levels were dimmer in Oslofjord than in other locations due to high amounts of dissolved organic matter. They calculated light levels at the upper boundary of the krill SSL in Oslofjord and found values ranging from 4.6×10^{-6} to 2.3×10^{-4} μmol m^{-2} s^{-1}, which are approximately the same light levels associated with *M. norvegica* in the Gulf of St. Lawrence (Sameoto 1980 – although no information is given on what wavelengths Sameoto was using). However, Onsrud and Kaartvedt utilized photosynthetically active radiation (PAR) meters for their subsurface light measurements, which measured downwelling irradiance over a range of wavelengths from 400 to 700 nm and calculated the irradiance at the euphausiid depth by estimating light extinction coefficients from irradiance measurements in the upper 30 m. Due to the wavelength-selective attenuation of seawater (Tyler 1958), the extinction coefficients calculated from PAR data will be too high (Gal et al. 1999). Therefore, calculated downwelling irradiance levels using these data will be significantly lower than the true irradiance in deeper water. When the values calculated by Onsrud and Kaartvedt are converted to photons cm^{-2} s^{-1}, the resulting irradiance is 2.8×10^{8}–1.4×10^{10}. To convert to photons cm^{-2} s^{-1} nm^{-1}, we used our own spectral measurements from Oceanographer Canyon (Widder and Frank 2001) to estimate the percentage of available light in the 480-nm waveband at depths below 100 m. Between 100 and 200 m, this value was approximately 2%, which means that the irradiance in the krill SSL estimated by Onsrud and Kaartvedt would be equivalent to 5.5×10^{6}–2.8×10^{8} photons cm^{-2} s^{-1} nm^{-1}at 480 nm. As expected, these values are substantially lower than the irradiance range associated with the leading edge of the *M. norvegica* population in our study – 10^{9}–10^{8} photons cm^{-2} s^{-1} nm^{-1} at 480 nm (480–490 nm are also the λ_{max} of euphausiid spectral sensitivity – Frank and Widder 1999). However, our data also underestimate the true irradiance available to the crustacean eye, which has a broader sensitivity than the 480 interference filter used on the LoLAR. We have taken measurements with the "shrimp filter" (see Materials and methods), but there is no way to calibrate this filter to give a true estimate of the downwelling irradiance. Therefore, we have presented irradiance values at 480 nm, which is a standard methodology and can be utilized by other authors to compare with their data. While our data do not provide evidence that euphausiids are following an isolume during their vertical migrations, the movement to shallower water during the influx to remain within a preferred irradiance range and the return to deeper water after the influx had ceased suggest that this is a distinct possibility.

An alternative hypothesis, that the trophic environment changed between water masses in a manner that would affect the daytime feeding depth, is not supported by the fluorescence data. There was no increase in maximum fluorescence during the influx (Fig. 3D) with respect to pre-influx or post-influx conditions. In addition, the fluorescence data measured during the influx and under post-influx conditions below 150 m depth,

when animal distributions changed by 100 m, are not significantly different (Fig. 4D), whereas fluorescence data measured under pre-influx and post-influx conditions, when animal distributions were the same, are significantly different.

Roe (1983) indicated that one of the criteria demonstrating that a zooplankton population might be migrating with an isolume is that the population must have a discrete depth distribution. Clearly, this is not the case with the zooplankton populations in this study. The three groups that were clearly affected by the change in downwelling irradiance – small euphausiids, sergestids, and salps – had fairly broad depth distributions and migrated to shallower water as a population during the influx. And, similar to Roe's study, their distributions cover several orders of magnitude in light intensity. However, as also observed by Roe, this does not mean that individual organisms could not be following an isolume during their diurnal vertical migrations, even if the population as a whole is not. As stated above, age classes within a species appear to be segregated as a function of size, and those at the shallower end of the distribution would be expected to follow a different isolume than those at the deeper end of the distribution. During our study, we were unable to get sufficient data on the sunset dives, so it is unclear whether the nighttime migration of the krill in Oceanographer Canyon is following an isolume.

The presence of diurnal vertical migration in *S. fusiformis* is controversial. Several investigators (Laval et al. 1992; Tsuda and Nemoto 1992; Sardou et al. 1996) have described *S. fusiformis* as a weakly or nonmigrating species, while others (Franqueville 1971; Wiebe et al. 1979; Madin et al. 1996) have found that *S. fusiformis* and *S. aspera* undergo large migrations to the surface at night. As stated in Materials and methods, we did not have sufficient data at night for statistical analysis and comparison, but our results demonstrate that while no salps were found shallower than 350 m on ten day dives, on the two night dives conducted at 150 m, they were present in quantities (0.148 and 0.286 salps m^{-3}) comparable to the maximum abundances found at deeper depths during the day. What is clear from our study is that these species of salps show strong responses to changes in downwelling irradiance during the day and appear to adjust their daytime depths to remain within a range of preferred irradiances.

The lack of an effect of decreased irradiance on the vertical distribution of the myctophid species during the day was surprising. *B. glaciale,* the most abundant myctophid in Oceanographer Canyon, is clearly a vertical migrator (Kaartvedt et al. 1988; Sameoto 1988; Giske et al. 1990) and was present in net tows taken in surface waters at night during our study. A number of studies have correlated the daytime depth of various fish species with light intensity (Woodhead 1966; Dickson 1972; Isaacs et al. 1974; Kampa 1976; Levy 1990; Appenzeller and Leggett 1995), and other studies have demonstrated that SSLs composed primarily of mesopelagic fish moved in response to short-term fluctuations in surface light (*Maurolicus muelleri* – Giske et al. 1990; Baliño and Aksnes 1993; Rasmussen and Giske 1994; Atlantic salmon – Huse and Holm 1993). However, the vertical distribution of *B. glaciale* seems to be considerably more extensive during the day than the species in the above study. While *M. muelleri*, a mesopelagic species co-occurring with *B. glaciale* in Masfjorden, western Norway, is found in discrete upper (juveniles) and lower (adults) SSLs, both of which responded to changes in surface light during the day, *B. glaciale* was not found in distinct scattering layers. It has a broader daytime depth distribution both in the Norwegian fjord (Kaartvedt et al. 1988; Giske et al. 1990) and off the Nova Scotia Shelf (Sameoto 1988), and it was therefore difficult to determine its response to a decrease in downwelling irradiance. In Oceanographer Canyon, the myctophid fish, most of which were *B. glaciale,* had a similar diffuse daytime distribution, with significant numbers found between 375 and 750 m. However, the sergestid shrimp population also has a broad daytime distribution, similar to that of the myctophids, and it clearly showed a migration to shallower waters during the influx. Therefore, in spite of its broad daytime depth distribution, the ascent of the myctophid population to shallower water should have been equally apparent. The fact that both the statistically significant portions of the population, as well as the shallowest and deepest individuals, were found at the same depths during normal and influx conditions indicates that these species were not affected by changes in downwelling irradiance during the day.

N. cara has been observed to undergo vertical migrations in Wilkinson Basin in the Gulf of Maine (Youngbluth et al. 1996) and in coastal waters off British Columbia (Mackie 1985) but did not appear to undergo vertical migrations in Oceanographer Canyon during this study. Although the data were insufficient for statistical analysis, we found no *Nanomia* on two night dives to 250 m or two night dives to 150 m, where other migrating species were present. Clearly, in our study, they were not correlated with an isolume, did not move up to shallower waters to follow a preferred irradiance range during the day, and showed no evidence of migratory behavior at night.

In summary, this study provides compelling evidence that the daytime depth distributions of several species of vertically migrating euphausiids, salps, and sergestids are controlled by downwelling irradiance. To evaluate whether these species are also following an isolume during their diurnal vertical migrations, further in situ studies of their migratory behavior at sunset are required.

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