Diel vertical migration of zooplankton in Lake Baikal and its relationship to body size

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Abstract

Light is the proximate factor triggering diel vertical migration (DVM) of zooplankton in both marine and freshwater systems. In highly transparent waters, avoidance of light by zooplankton, and hence avoidance of visual predators, should be especially pronounced. Lake Baikal in south central Siberia is one of the clearest lakes in the world with Secchi disc readings ranging from 4 to more than 20 m in the summer. Assuming that smaller zooplankton are less visible to fish predators than larger taxa, we predicted that the copepod, *Epischura baicalensis*, should migrate into the upper water layers earlier in the evening than the larger members of the zooplankton fauna -- the pelagic gammarid, *Macrohectopus branickii,* and the juvenile fish, *Comephorus* spp. Closing net samples were collected at three depth layers within the top 50 meters of the water column at dusk, midnight, and midday in the southern basin of Lake Baikal in August, 2003. Consistent with our hypothesis, *Epischura* ascended first at dusk, whereas *Macrohectopus* and the juvenile golymyanka were detected in the top 50 meters of the water column only at midnight. Position in the water column and timing of migration was not associated with changes in water temperature, however, movement of *Epischura* into the top 10-m may have been influenced by small changes in chlorophyll abundance between sampling periods. Finally, differences in the timing of ascent of these taxa into the upper surface waters may also be explained by their differing abilities to escape fish predators once detected. The sensitivity of these zooplankton taxa to a sudden increase in light at night was tested experimentally, and results revealed that *Macrohectopus* left the illuminated area rapidly and abundance of adult *Epischura* declined 40%. The negative phototactic behavior of these species may protect them when suddenly exposed to visual fish predators such as occurs when the moon emerges abruptly from cloud cover.

Introduction

Diel vertical migration (DVM) of zooplankton is a widespread behavioral phenomenon that occurs in lakes and the ocean. The typical, ‘nocturnal’ pattern of DVM consists of zooplankton residing deep in the water column during the day, ascending at dusk to shallower depths where they feed, and returning at dawn to deeper daytime depths (Hutchinson 1967). Although avoidance of visual predators and harmful UV-radiation seem to be the ultimate causes of DVM (Lampert 1989, 1993; Ringelberg 1999; Leech & Williamson 2001), light is the proximate factor eliciting this behavior (Haney 1993; Ringelberg 1999). Specifically, the rate of change of light intensity is the proximate cue that triggers the ascent of zooplankton at dusk and their descent at dawn (Ringelberg 1964;1995).

In oligotrophic systems with highly transparent waters, light penetrates more deeply. Here, zooplankton DVM should be especially pronounced because risk to visual predators and exposure to UV-radiation is potentially much greater than in less clear waters. Lake Baikal in southcentral Siberia is among the clearest lakes in the world with Secchi disc readings sometimes exceeding 20 meters in the summer (Kozhova and Izmest'eva 1999), and the dominant members of the crustacean zooplankton exhibit strong ‘nocturnal’ patterns of DVM in August and September (Kozhova & Izmest’eva 1999).

In midsummer, three taxa dominate the zooplankton fauna of the pelagic waters of Lake Baikal, and these organisms range widely in size. The endemic copepod, *Epischura baicalensis* (adult length 1.6 mm), is the smallest, and it is consumed by the pelagic gammarid, *Macrohectopus branickii* (10 - 15 mm; this study). The largest member of the zooplankton in Lake Baikal is the juvenile golomyanka, *Comephorus* spp. (30 - 40 mm; this study), a fish which feeds mainly on *E. baicalensis* (Yoshii et al. 1999). In summer, all three taxa are consumed heavily by visual fish predators including the omul (*Coregonus autumnalis migratorius*) and pelagic sculpins (*Cottocomephorus* spp.) (Kozhova & Izmest'eva 1999). Adults of the most abundant fish in the lake, the golomyanka (*Comephorus* spp.; body length, > 40 mm), feed primarily on *Macrohectopus* and larval sculpins, but not *Epischura* (Yoshii et al. 1999). During the short period of relatively warm water temperatures in summer (i.e., August and September), fish predation is intense (Kozhova & Izmest'eva 1999), and it is likely an ultimate factor driving zooplankton DVM in Lake Baikal.

In this paper, we test the hypothesis that the timing of ascent into the upper surface waters at night by macrozooplankton in Lake Baikal varies with body size. Larger. rather than smaller prey, are more vulnerable to visual predators who feed most efficiently in upper surface waters when light is adequate for prey detection. Hence, we predicted that the smaller taxon, *Epischura baicalensis*, would rise to the surface earlier in the evening than *Macrohectopus* and the juvenile golomyanka. Due to their larger sizes, *Macrohectopus* and the juvenile golomyanka should be more vulnerable to visual predators than *Epischura*. Consequently, these larger taxa should rise later at night when light levels are sufficiently low that visual predation is lessened. We tested this hypothesis by collecting closing net samples at multiple depths in Lake Baikal at dusk, night, and midday. In addition, we tested the response of these zooplankton taxa to artificial light at night to assess their sensitivity to a sudden increase in light intensity comparable to that caused by the moon suddenly emerging from behind clouds.

Methods

Our sampling site was located in the southern basin of Lake Baikal approximately 1 km northeast of Bol'shie Koty (52º 15'N, 105º 10'E). Water depth at the sampling station was approximately 400 m. Samples were obtained on 3 - 4 August, 2003 at dusk (21:30-22:30), midnight (01:00 - 2:30) and at midday (11:30 -12:30). Using a closing net (80μm mesh; 40-cm diam), two replicate vertical tows were taken through each of three depth layers (0 - 10, 20 - 30, and 40 - 50m) during each sampling period. In addition, water temperature and chlorophyll *a* were measured using a YSI sonde at 0 and 5 m and every 10 m down to approximately 40 m at noon and to 50 m at dusk. At noon, no chlorophyll measurements were obtained at the surface. During the investigation, the sky was clear, water conditions calm, and at night, a moon approaching first-quarter was located approximately 30° above the horizon for 2 hrs after darkness.

To assess the response of the zooplankton to a sudden increase in light intensity, a bright lamp (approximately 100 watts) was shone on the surface of the water during the midnight sampling period for 20 min prior to sampling. Two zooplankton samples were then collected in the 0 - 10 m water layer with the closing net. All other midnight samples (described above) were collected in the dark before the light experiment. During the midnight (i.e., darkness) sampling, all boat lights were extinguished except for a single light at the top of the mast. Illumination from this mast light was sufficiently weak that a flashlight was needed to operate the winch controlling the depth of the closing net.

Macrohectopus and juvenile golomyanka were separated from each sample and counted by eye. *Epischura* adults (copepodites were included in counts of adults) and nauplii, however, were counted in 0.5 ml-subsamples using a dissecting microscope at 20X magnification. At least three subsamples per sample jar were counted, and the coefficient of variation of subsampling was rarely more than 0.20. Mean densities (no. per liter) of *Epischura*, *Macrohectopus*, and golomyanka were calculated by averaging subsampling means for each of the two samples collected at each depth and time.

Results

Epischura baicalensis ascended earlier in the evening than either *Macrohectopus* or juvenile golomyanka. At dusk, *Epischura* densities in the top 30 m of the water column were almost double that observed at the 40 - 50 m depth layer (Figs. 1 & 2), but neither *Macrohectopus* nor juvenile golomyanka were present in the top 50 m of the water column (Fig. 3). By 01:00, both *Macrohectopus* and juvenile golomyanka had risen into the top 50 m of the water column. *Macrohectopus* was present in the greatest abundance in the top 10 m (0.007 individuals/L), whereas the larger golomyanka occurred only at depths of 20 m or less (Fig. 3). At midday, *Macrohectopus* and juvenile golomyanka were absent from the top 50 m of the water column (Fig. 3), and far fewer *Epischura* were present in the top 10-m water layer than at dusk or midnight (Figs. 1 & 2). Specifically, densities of adult *Epischura* and nauplii were 97 - 98.5% lower in the top 10 m water layer at midday than at dusk or midnight .

Densities of *Epischura* and *Macrohectopus* declined in the top 10 m water layer after the 20-min exposure to artificial light at night (Fig. 4). Mean densities of adult *Epischura* declined by 40% in response to the illumination, whereas mean densities of nauplii declined only 27%. *Macrohectopus* was present at low numbers (0.007/l) when lights were off, but it vacated the 0 -10 m water layer after exposure to artificial light.

Water temperature never varied more than 1°C throughout the top 50 m of the water column, however, chlorophyll concentrations tended to increase with depth (Fig. 5). Water temperatures ranged from 4.8°C at the surface to 4.4 °C at 48 m at dusk on 3 August, 2003. During the midday sampling period on 4 August, the water surface warmed to 5.5 °C but at all other depths, temperatures ranged from 4.4 - 4.5°C. Chlorophyll concentrations were low and less than 1 mg/m^3 throughout much of the column during the dusk and midday sampling periods. At midday on 4 August, 2003, chlorophyll concentations were zero at 5 m but increased to a maximum of 0.8 mg/m^3 at 28 m. Secchi disc transparency was 23 m on 4 August, 2003 at a nearby monitoring station located 1800 m offshore from Bol'shie Koty (Liubov' Izmest'eva, personal communication).

Discussion

Consistent with our hypothesis, the smaller *Epischura baicalensis* ascended earlier into the upper surface waters of Lake Baikal than did the larger *Macrohectopus* and the juvenile golymyanka. Indeed, the latter two taxa did not appear in the top 50 meters of the water column until the midnight sampling period. It could be argued that the delayed ascent of *Macrohectopus* and the juvenile golymyanka is not correlated with body size and predation risk, but is simply the consequence of their deeper position in the water column during the daytime. For example, during the day, *Macrohectopus* adults and immature females aggregate at depths between 100 and 200 m (Melnik et al. 1993), whereas *Epischura* typically congregates between 10 and 50 m (Kozhov 1963 as cited by Kozhova & Izmest'eva 1999). Thus, *Macrohectopus* has a greater distance to ascend at night than *Epischura*, and this may explain the former's later appearance in the surface waters at night. Countering this argument, however, is the rapid speed at which *Macrohectopus* vertically migrates. At night, it moves upwards at a speed of 4 m per minute (Melnik et al. 1993); thus it would take *Macrohectopus* only 30 min to travel 120 m, placing much of the population in the top 50-m water layer quickly. Finally, the deeper depth position occupied by *Macrohectopus* and the juvenile golymyanka during the day could also be a result of their increased vulnerability to visual fish predators relative to that of *Epischura*. These former two taxa may position themselves at deeper depths where irradiance during the day is at levels where visual fish predation on larger prey is minimized. This could be tested by comparing the feeding efficiency of Lake Baikal's visual fish predators on each of these three prey taxa at daytime light intensities typical of the water depths at which each prey taxa aggregates during the day.

Alternatively, the differential timing of the DVM ascent of these zooplankton taxa may correlate better with their escape responses to fish predators than with their body size. The jumping response of copepods when approached by fish predators is well documented (e.g., Confer & Blades 1975; Drenner et al. 1978), and it helps explain why copepods are less vulnerable to fish predators than non-jumping prey such as large cladocerans. *Macrohectopus* lacks an escape response and adult golymyanka are noted for their sluggish movements (Eugene Silow, personal communication). Consequently, *Epischura*, by virtue of its escape behavior, should be the least vulnerable of these three prey taxa to fish predators, thereby allowing *Epischura* to remain near surface waters during the day and to ascend into upper waters as levels of solar illumination drop. Suggestions that low water temperatures (<15 °C) slow the evasion of copepods to visual fish predators (O’Brien 1979), however, may compromise the applicability of this explanation to the cold waters of Lake Baikal. Finally, *Macrohectopus* and the juvenile golymyanka may be so vulnerable behaviorally to visual fish predators that ascent into the upper surface waters (i.e., upper 50 m) occurs only when predation risk is reduced to very low levels by conditions of complete darkness.

Finally, it should be noted that the abundance of food may have influenced the depth position and timing of at least one of these three zooplankton taxa -- *Epischura baicalensis*. Algal abundance was below the detection limits of the fluorometer at 5 m at midday when *Epischura* adults and nauplii were nearly absent from the 0 - 10 m layer. In contrast, at dusk, when *Epischura* moved up into the 0 - 10 m layer, chlorophyll levels were higher ranging from 0.5 to 0.8 mg/m3 in the top 10 m. Thus, the tracking of algal food abundance may have led *Epischura* into the near surface waters in the evening.

Results of the artificial light experiment showed that adult *Epischura* and *Macrohectopus* respond quickly, within 20 min, to an abrupt increase in illumination at night. The sensitivity of adult *Epischura* and *Macrohectopus* to illumination at night suggests that their negative phototactic behavior may protect them against sudden exposure to visual predators at night such as may occur when the moon emerges abruptly from cloud cover. It is interesting to note that few studies of vertical migration in Lake Baikal have focused on zooplankton community responses to changing light levels. However, competition for food in ultraoligotrophic lakes may make such competition intense, emphasizing the importance of individual fitness of early diel migration.

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Figure Captions

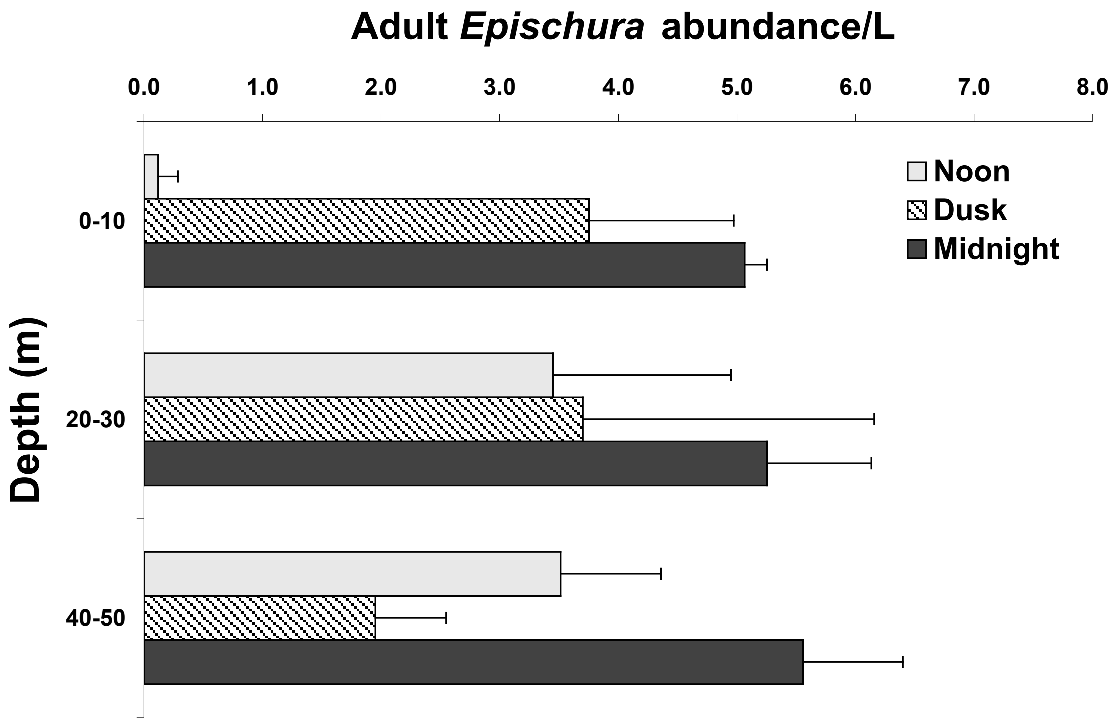
Fig. 1. Abundance of *Epischura baicalensis* adults (no./L) at three depths in the southern basin of Lake Baikal at dusk, midnight and noon on 3-4 August, 2003.

Fig. 2. Abundance of *Epischura baicalensis* nauplii (no./L) at three depths in the southern basin of Lake Baikal at dusk, midnight and noon on 3-4 August, 2003.

Fig. 3. Distribution by depth of *Macrohectopus branickii* and juvenile golomyanka (*Comephorus* spp.) at midnight in the southern basin of Lake Baikal on 4 August, 2003. These species were not found in samples collected at noon or dusk.

Fig. 4. Abundance of zooplankton taxa in the 0 – 10 m depth layer in Lake Baikal before (Lights off) and after (Lights on) illuminating the water's surface with a 100-watt lamp for 20 min at night. This experiment was performed on 4 August, 2003 at a sampling station located approximately 1 km northeast of Bol'shie Koty.

Fig. 5. Depth distribution of chlorophyll (mg/m^3) and temperature (°C) at noon and dusk on the dates that zooplankton were sampled in Lake Baikal (see text). At noon, no chlorophyll measurements were obtained at the water surface.



Adult *Epischura* abundance/L
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
Noon
Dusk
Midnight
Depth (m)
0-10
20-30
40-50

Fig. 1

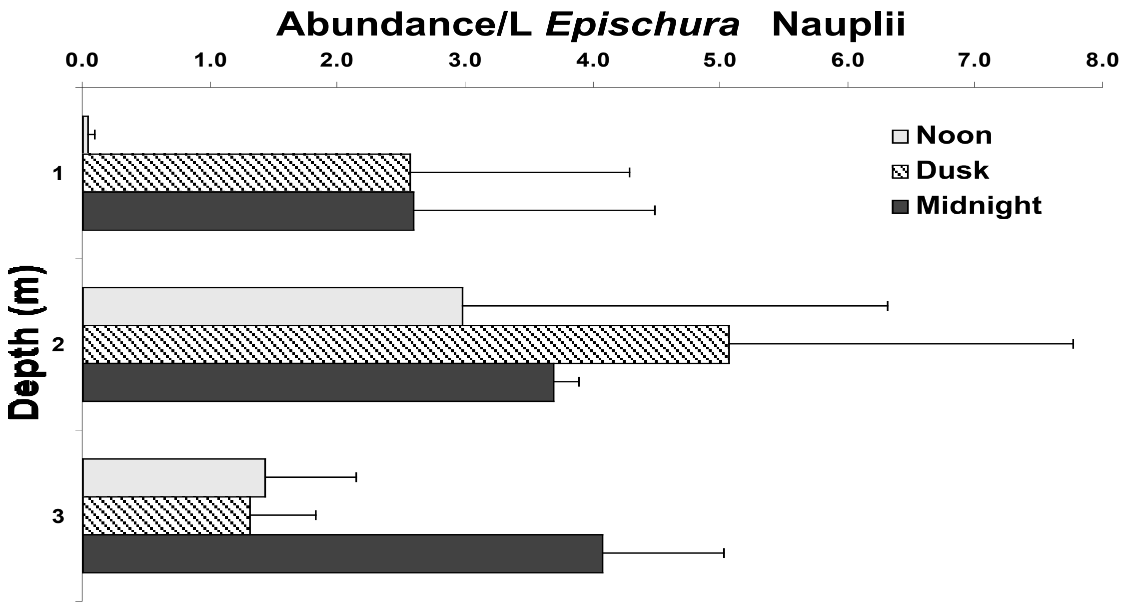
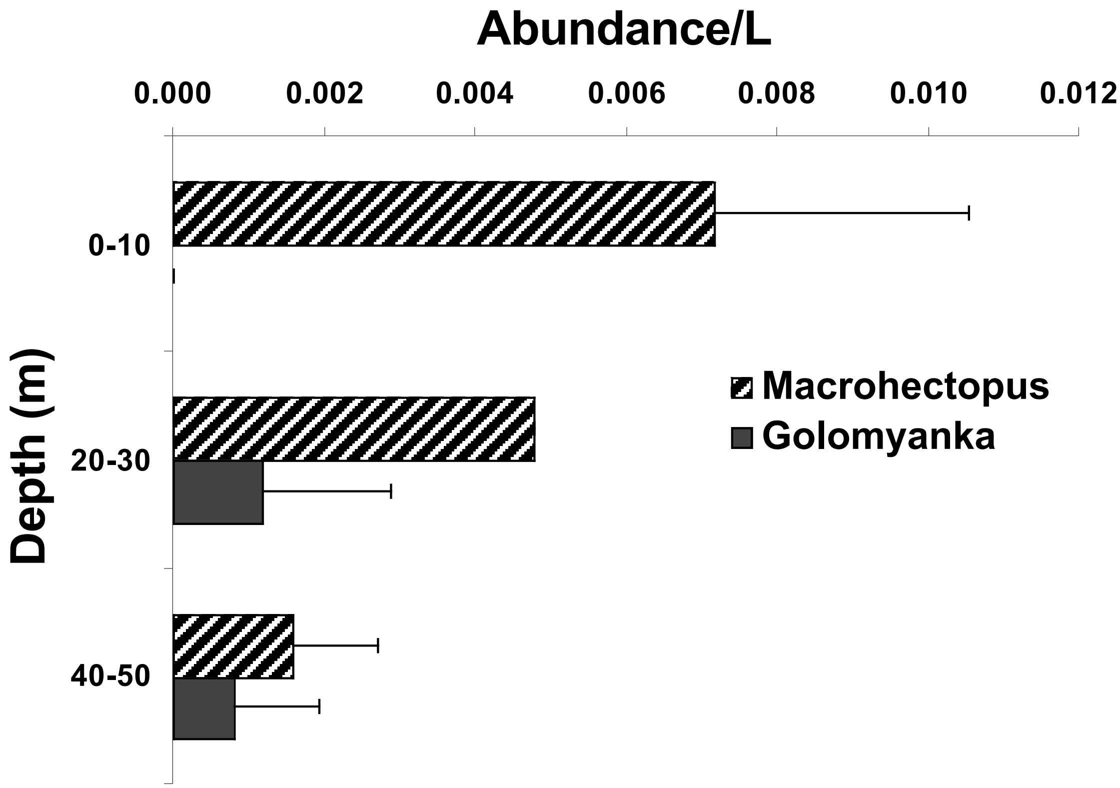

Abundance/L *Epischura* Nauplii
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
Depth (m)
1
2
3
Noon
Dusk
Midnight

Fig. 2



Abundance/L
0.000
0.002
0.004
0.006
0.008
0.010
0.012
Depth (m)
0-10
20-30
40-50
Macrohectopus
Golomyanka

Fig. 3

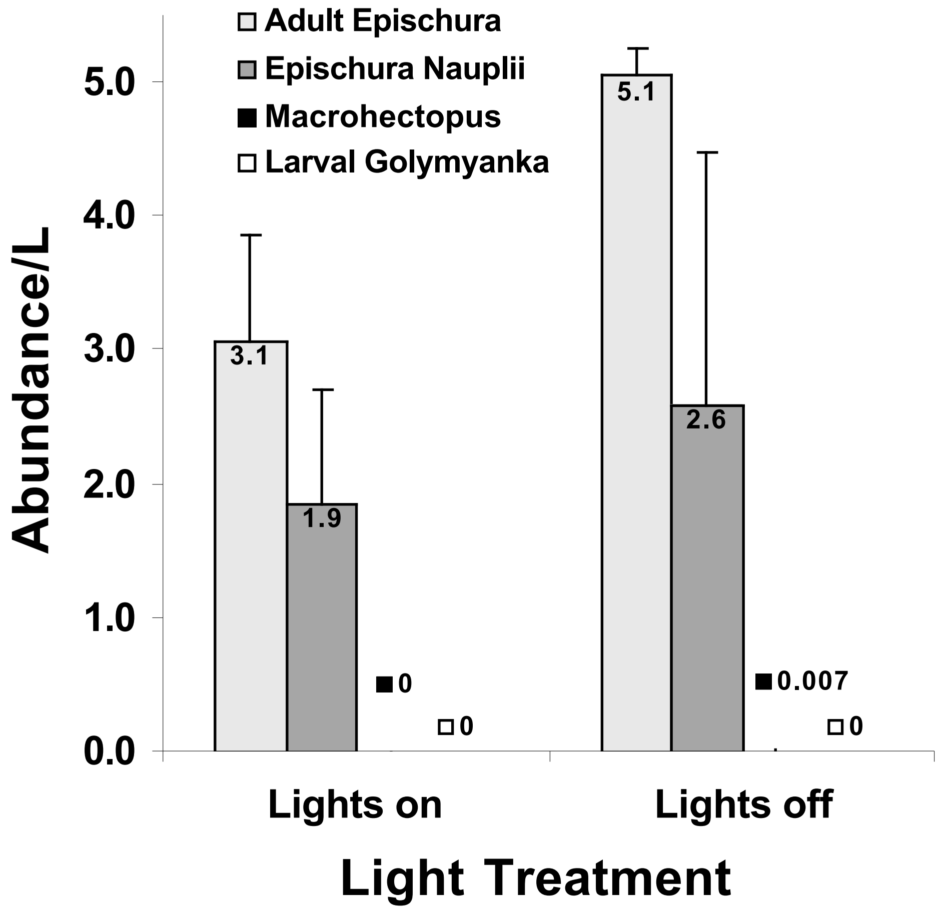

Adult Epischura
Epischura Nauplii
Macrohectopus
Larval Golymyanka
Abundance/L
5.0
4.0
3.0
2.0
1.0
0.0
3.1
1.9
0
0
5.1
2.6
0.007
0
Lights on
Lights off
Light Treatment

Fig. 4.

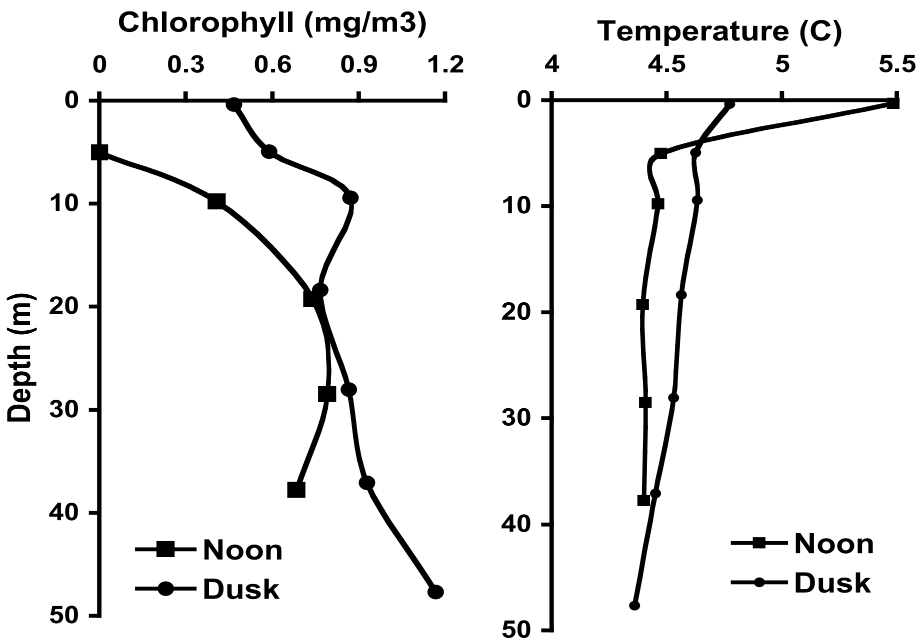

Chlorophyll (mg/m3)
0
0.3
0.6
0.9
1.2
Depth (m)
0
10
20
30
40
50
Noon
Dusk
Temperature (C)
4
4.5
5
5.5
0
10
20
30
40
50
Noon
Dusk

Fig. 5.