Vertical migration of marine copepods in the Galapagos Islands in relation to size and color

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Running Header: Vertical migration of copepods in relation to size and color

Non-technical Summary

Diel vertical migration (DVM) is widespread among both freshwater and marine zooplankton. Patterns of diel vertical migration can vary between and within species, and under different environmental conditions. This study examined the relationships between the vertical migration pattern of copepods and their body conditions in term of body size and body coloration. Zooplankton samples were collected by net sampling at 145 m-deep location (0° 37′ S, 91° 19′ W) and 1100 m-deep location (0° 37′ S, 91° 25′ W) in the western regions of the Galapagos Islands on 14-15 January 2006. Copepod abundance, body length, and color were examined. Day/night difference in the vertical distribution of copepods abundance was observed at the shallow station as a result of vertical migration behavior, but no apparent trends of copepod migration was observed as a whole at the deep station. Variability in DVM was observed among specific copepod groups. For individuals that were found in the upper 40 m in the daytime, the average body size was slightly larger than those that remained at depth and vice versa for night time. Similarly, colored copepods were found to be more concentrated in the surface waters during the day and more concentrated at depth at night. Migration of the colored and/or large copepods from the surface waters to the depth at night has been exhibited. All these observations show that individual body condition of copepod is directly related to their vertical migration. Based on their body condition, copepods modify their migration pattern in response to their predators.

Acknowledgments

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Abstract

Patterns of diel vertical migration (DVM) can vary remarkably between and within species, and under different environmental conditions. This study explored the relationships between the vertical migration pattern of copepods and their body size and coloration. DVM of copepods was examined by repeated day-night sampling at 145 m-deep location (0° 37′ S, 91° 19′ W) and 1100 m-deep location (0° 37′ S, 91° 25′ W) in the western regions of the Galapagos Islands on 14-15 January 2006. Day/night difference in the vertical distribution of copepods abundance was observed at the shallow station as a result of vertical migration behavior, but no apparent trends of copepod migration was observed as a whole at the deep station. Variability in DVM was observed among specific copepod groups. For individuals that migrated to the surface in the daytime, mean prosome length was slightly larger than those that remained at depth and vice versa at night. Similarly, pigmented copepods were found to be more concentrated in the upper 40 m during the day and were more concentrated below 100 m at night. With the demonstration of reverse vertical migration by the pigmented and/or large copepods, these results suggested that individual variability in DVM was influenced by body conditions. Based on their body condition and environmental stimuli, copepods modify their migration pattern in response to their predators.

Introduction

Diel vertical migration (DVM) is a common behavioral phenomenon that occurs in both freshwater and marine zooplankton. Three general patterns of DVM have been recognized, the most common one is an ascent to the surface around sunset and descent to the depth around sunrise, known as normal DVM. Another pattern involves an ascent to the surface at sunrise and a descent to the depth at sunset, known as reverse DVM. The third pattern involves an ascent to the surface at sunset, a descent to deeper water around midnight, followed by a second ascent to the surface and then descent to deeper water around sunrise, termed twilight DVM (Cohen and Forward. 2002). The pattern that is performed can vary remarkably between and within species and under different environmental conditions.

Many possible mechanisms underlying DVM have been proposed, among which the predator-avoidance hypothesis has received the most attention. This hypothesis suggests that zooplankton perform migration to avoid visual predators and to reduce the risk of mortality. Light (sunlight and moonlight) as a visual cue can have strong influences on the avoidance behavior (Liu et al. 2003). The lower ambient light levels near the surface at night make it harder for visual predators to perceive their prey, thus lowering the risk of predation. Both normal and twilight DVM provide a daytime refuge from visual predation in dim light areas at depth and night-time access to food-rich surface water. Reverse DVM provides protection from nocturnally migrating predators (Hays 2003). The predator-evasion hypothesis thus suggests that DVM is related to prey visibility (Zaret and Suffern 1976), which should increases with size and body pigmentation, causing greater susceptibility. Previous studies on the vertical distributions and migrations of the zooplankton have shown that the size of marine copepods has a significant influence on their vulnerability to predation. Moreover, the marine copepods most susceptible to visual predation due to conspicuous coloration and large body size exhibited a greater vertical migration response (Hays at el. 1994; Pearre 2003; Suchman and Sullivan 2000).

Variations in individuals' conditions such as body size, oil sacs size, body pigmentation and fullness of the gut, and environmental conditions such as food availability, water depth, light penetration and bottom topography may cause difference in migration behavior. For the present study, I examined the vertical migration of copepods in relation to their body size and coloration in two different water depths in the western regions of the Galapagos Islands, where productivity is generally high. Copepods with larger body size and greater coloration were hypothesized to exhibit stronger migrations to avoid being seen by their predators, thus the abundance of the large and/or pigmented copepods was expected to be high in surface waters at night and high in deeper water during the daytime.

Previous scientific studies in the Galapagos Islands found that the western region of the Islands (along the west coast of Isabela and Fernandina) is the most productive due to the upwelling of the equatorial undercurrent, which brings nutrients up to the surface and enriches the surrounding surface waters (Chavez and Brusca 1991). Copepods are found to be the most abundant organisms, making up at least 90% of the zooplankton in the Galapagos waters (Roman et al. 1997). With a diverse assemblage of zooplankton numerically dominated by copepods, zooplankton data acquired will not only provide better understanding of the migrational behavior and the biological interaction of copepods in the Galapagos regions, but will also give insight into the role of visibility in diel vertical migration and, by inference, the effects of predators on the zooplankton community.

Materials and Methods

Sampling was carried out aboard the *R/V Thomas G. Thompson* at 145 m-deep location (0° 37′ S, 91° 19′ W) and 1100 m-deep location (0° 37′ S, 91° 25′ W) in the western regions of the Galapagos Islands on 14-15 January 2006 (Fig. 1). Each sampling site was visited twice for repeated day and night sampling; at the first visit to a given station, temperature, fluorescence, and light intensity were recorded with the SeaBird SBE9/11 CTD before net sampling. Each sampling event occurred at roughly the same time for each day and each night (Table 1). Zooplankton samples were collected from three discrete depths (145 m-deep station: 0-40 m, 40-100 m, and 100-140 m; 1100 m-deep station: 0-40 m, 40-100 m, 100-180 m) using a vertically deployed opening/closing net with a mouth diameter of 1 m and mesh size 335 μm. Each haul was lowered and retrieved at roughly 30 m/min.

In the laboratory, zooplankton samples were split into four "equal" portions using a Folsom plankton splitter, and were shared with other scientists on board for their zooplankton study. Samples were preserved with 4% formaldehyde in 250 ml labeled glass jars for subsequent analysis. 5.0 ml subsample was taken from each 250 ml sample jar; copepods were picked out and counted for abundance under a dissecting microscope. Each subsample was counted twice to get a more precise estimate of abundance. To examine coloration, colors of the copepods were noted while counting. Copepods that showed color from their gut content, their internal oils, or exoskeleton were noted as “pigmented”; others were noted as “clear”. A few representatives from each color group were photographed through the eyepiece of the compound microscope using a Canon PowerShot A95 camera (5.0 megapixels). No flash was used. To determine the size distribution of the copepods in the subsamples, prosome lengths (Fig. 2) were measured from the tip of the head to the insertion of spines into the caudal ramus under the compound microscope. Prosome lengths that were measured were used to quantify the size of the remaining copepods in the subsamples.

Results

Vertical Distribution

At the shallow station (JN-S) where the water depth is about 145m, day/night changes in the vertical distribution of copepod abundance between 0 m and 140 m were observed. Copepods were found mostly in the upper 40 m for both day and night (Fig. 3a). At night, the abundance of the copepods was increased by about 90% in the upper 40 m (Table 2), and a slight decrease was observed in the lower 100 m (Fig. 3a). The total abundance of the copepods was about 40% higher at night compared to the daytime (Table 2).

At the deep station (JN-D) where the water depth is about 1100 m, the day/night vertical distributions of the copepods were fairly similar (Fig. 4). Copepods were most numerous in the upper 40 m of the water column during both day and night, and with decreasing number of individuals toward the bottom (Fig. 3b). However, the data showed a significant decrease in the copepod abundance in the upper 40m at night on 15 January 2006 (Fig. 4).

Size Distribution

At JN-S, differences in day/night size distribution of copepods were observed. Prosome length was slightly longer for individuals in the upper part of the water column (between 0-40 m) during the day and decreased with depth. Conversely, at night, the prosome length of copepods in the upper 40 m was slightly shorter than those below 40 m (Fig. 5a). At JN-D, only slight size difference was observed throughout the water column, except the prosome length was greater for copepods between 40-100m during daytime. At night, no significant difference in mean prosome length was found throughout the water column (Fig. 5b).

Color Distribution

At JN-S, changes in the color distribution over the water column during day and night were observed. The data showed an increase in the colored copepods in the lower water column and a decrease in the surface waters at night (Table 2). About 71% of the copepods collected at the upper 40 m during the daytime were pigmented (Fig. 6a). In contrast, most pigmented copepods were found below 40 m at night; about 73% of the copepods collected between 100-140 m were pigmented. At JN-D, water column from 0 -180 m was dominated by non-pigmented copepods for both day and night, but changes in vertical distribution of pigmented copepods were observed. There were more pigmented copepods found in the upper 40 m during the day and less at night; an increased number of pigmented copepods in the lower 100 m was found at night (Fig. 6b).

Discussion

While predation pressure could be a reason behind the zooplankton vertical migration, environmental and individual variations can also be factors that drive the vertical migration. JN-S had a water depth of 145 m, and was located above the continental shelf. No active diel vertical migration is generally present in the neritic environment (Banse 1964) where the water depth is too shallow for them to perform vertical migration. Vertical migration by copepods at JN-S could have been limited by such environment. However, an increase of 90% in the copepod abundance in the upper 40 m at night and a slightly change in the abundance between 100 and 140 m (Fig. 3a) was in fact consistent with DVM. Changes in the total abundance between day and night suggest that copepods found in the upper 40 m at night could have come from somewhere below 140 m. Because it is hard to determine the numbers of individuals that remain in close association with the seabed, it is unclear about where exactly the copepods came from.

Copepods could either remain in the seabed or hide inside the feature that was on the continental shelf during the daytime. Decreases in surface catches during the daytime may be due to daytime net avoidance, however, it is restricted to animals with advanced visual system such as euphausiids, and it is not seen in those with simpler eyes like copepods (Miller 2004).

The average data from two sampling days showed no conspicuous day/night difference in the vertical distribution of copepods at JN-D, which implies there was no vertical migration at the deep station. However, the abundance of the copepods during the night sampling was found to coincide with the moonlight. During the first night sampling event (14 January 2006), the moon was covered by clouds, this date displayed a higher abundance of total copepods (m^{-3}) in the upper 40 m; significantly there was a decrease in copepod abundance on the second date of night sampling (15 January 2006) when the moon was visible (Fig. 4). These imply that moonlight could play a role in driving DVM (Cohen and Forward 2002).

Copepods appeared to be concentrated mainly in surface waters (upper 40 m) where the chlorophyll concentration was high (Fig. 7a, 7b), this finding is similar to that of White et al.(1995) for the tropical Pacific. Staying in the upper column during the day would place those copepods in a light environment adequate for vision, while also allowing them to maintain their horizontal position over the continental shelf without being transported too far inshore or offshore (Tester et al. 2004). Of the copepods found in the surface layers during the day, most of them were pigmented (Fig. 8a). Instead of migrating down to the depth, they remained in the surface waters. Mobility increases the retinal area stimulated, hence preys that are moving will be sighted at a greater distance than non-moving preys, so motion generally increases the risk of predation (Eggers 1977). Increased prey motion has also been shown to increased the encounter rate (Werner and Anholt 1993), so reduced activity/motion could actually be an anti-predation strategy useful to both pigmented and transparent organisms. These could explain the high abundance of larger and/or pigmented copepods found in the upper water column during the daytime.

Copepods that have conspicuous coloration should exhibit greater normal vertical migration response due to their visibility, but the opposite was also observed. Pigmented copepods were actually found abundant in the upper water column during the day and migrated down to the depth at night (Fig. 6). Hay et al. (1994) suggested that copepods that could easily escape detection due to camouflage coloration remained in surface waters during the day, so they exhibited no migratory response to predation pressure. Light attenuation increased at high phytoplankton concentrations in the upper surface waters (Fig.7), which would definitely affect the visual predation efficiency, so at high phytoplankton densities, the migrations may actually decrease (Fiksen and Giske 1995), and the risk of predation would be lower for those pigmented copepods as long as they remain within that layer. The reverse migration observed in the pigmented and/or large copepods (Fig. 5a, 6) may be induced by the presence of visual predators (eg. chaetognaths and euphausiids) that were either undergoing nocturnal DVM or avoiding the net during daytime samplings. Euphausiids were found exclusively in the night samples for both shallow and deep stations during 14-15 January 2006 (Nomura, pers. comm.), which imply that the observed reverse migration may be employed as a defense against other vertical migrating zooplanktons. Such behavior has been clearly documented in the marine environment for some copepods, which undergo reverse DVM when other predatory copepods, chaetognaths, and euphausids are present and are migrating nocturnally (Tester et al. 2004).

Transparent copepods (Fig. 8b) were found mostly below 40 m (Fig. 6); this could be explained by the light-protection hypothesis, which states that downward migration of zooplankton is performed to avoid the harmful UV light that penetrates the surface waters in daylight hours (Leech and Williamson 2001). Pigmented copepods are less sensitive to visible light and more likely to survive in light than the non-pigmented ones (Ringelberg 1980), which suggested that transparent copepods tend to exhibit downward migration during daylight and upward migration at night.

Since a substantial amount of variation occurs within the migrating behaviors of copepods, it may not be possible to explain this variation through a theory that considers only one or two type of responses. The variability in vertical distribution among the copepods at least partly can be explained by differences in body conditions. Regarding them as exclusively food-controlled, predator-controlled or light-controlled will certainly oversimplify the migratory behavior of the copepods; further study is required to resolve all those mechanisms underlying DVM. Results drawn from two-day samplings are definitely insufficient to explain such a complex behavior; multiple samplings through the light and dark periods and acoustical surveying would definitely help to validate the data. Besides, marine environments may need to be considered in order to gain a better understanding of vertical migration, for example, abrupt changes in bottom topography can also affect the vertical migration of copepods, so it's necessary to also examine the bottom topography along with the copepod data, especially at a shallow station like JN-S. To further examine the relationship between individuals' body condition and migration pattern, more parameters needed to be taken into account, such as gut fullness, oil sac length and volume, status of being ovigerous or non-ovigerous, and egg mass; those could all contribute to the prey visibility beside body pigmentation and body length.

Conclusion

Diel vertical migration by zooplankton is a universal feature in all the world's oceans. The relative diversity and complexity of vertical migration makes it hard to find a unifying theory to explain the variations in migration patterns exhibited by zooplankton species. Although this study focused particularly on copepods, it is generally applicable to other zooplankton. Evidence consistent with DVM by copepods in general was found at the shallow station but not the deep station, which suggested that zooplankton vertical migration could possibly depend on the environments. With the presence of nocturnal migrating predators, reverse DVM was demonstrated by the large and/or pigmented copepods at both shallow and deep stations, which implied that individual variability in DVM was influenced by body conditions as well as predation. Patterns and amplitude of DVM could actually vary between and within species. As suggested by the results, both environmental and individual body conditions can be critical in modifying the vertical migration of the copepods, and predation pressure is indeed a major driving force behind DVM. The data acquired in this study do not only give insight into the role of body conditions in diel vertical migration, but also provide better understanding of the effects of predators on the zooplankton community.

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Tables and Figures

Table 1. Sampling locations and times during 14 – 15 January 2006

Date		Station	Depth (m)	Time (GMT)	Local Time
14 Jan 06	AM	JN-D [*]	100-180	16:26	10:26 AM
			40-100	16:49	10:49 AM
			0-40	17:04	11:04 AM
		JN-S [†]	100-140	18:59	12:59 PM
			40-100	19:02	1:24 PM
			0-40	20:04	2:04 PM
	PM	JN-D	100-180	03:06	9:06 PM
			40-100	03:29	9:29 PM
			0-40	03:46	9:46 PM
		JN-S	100-140	05:48	11:48 PM
			40-100	06:12	12:12 AM
			0-40	06:30	12:30 AM
15 Jan 06	AM	JN-D	100-180	14:38	8:38 AM
			40-100	14:53	8:53 AM
			0-40	15:30	9:30 AM
		JN-S	100-140	16:17	10:17 AM
			40-100	16:33	10:33 AM
			0-40	16:49	10:49 AM
	PM	JN-D	100-180	03:07	9:07 PM
			40-100	03:26	9:26 PM
			0-40	03:40	9:40 PM
		JN-S	100-140	04:49	10:49 PM
			40-100	05:05	11:05 PM
			0-40	05:19	11:19 PM

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[*] JN-D: 1100 m-deep station

[†] JN-S : 145 m-deep station

Table 2. Estimated abundance of the copepod at JN-D and JN-S during day-night sampling, and the percentage each color contributes to each sample.

	Sample #	**Depth (m)**	**Color (%)**	**Clear (%)**	**Individuals per m^3**
JN-D	AM-1	0-40	62%	38%	136
		40-100	10%	90%	14
		100-180	13%	87%	12
	AM-2	0-40	37%	63%	100
		40-100	27%	73%	37
		100-180	35%	65%	9
	PM-1	0-40	19%	81%	141
		40-100	21%	79%	13
		100-180	44%	57%	12
	PM-2	0-40	31%	69%	64
		40-100	29%	71%	29
		100-180	36%	64%	7
JN-S	AM-1	0-40	75%	25%	67
		40-100	44%	56%	22
		100-140	31%	70%	25
	AM-2	0-40	68%	32%	56
		40-100	39%	61%	24
		100-140	50%	50%	33
	PM-1	0-40	62%	38%	126
		40-100	55%	45%	25
		100-140	65%	35%	24
	PM-2	0-40	39%	61%	108
		40-100	60%	40%	26
		100-140	81%	19%	14

Figure Legends

Figure 1. Location of the two sampling sites, JN-S and JN-D, in the Galapagos Islands.

Figure 2. General morphology of Copepoda (Carling et al. 2004), prosome length is showed.

Figure 3. Comparisons based on vertical net tows of day and night vertical distributions of copepods at stations (a) JN-S (145 m-deep) and (b) JN-D (1100 m-deep) in the Galapagos Islands during 14-15 January 2006.

Figure 4. Day and night vertical distributions of copepods during two different sampling day, 14 and 15 January 2006 at JN-D.

Figure 5. The mean prosome length of the copepods at different depths at stations (a) JN-S (145 m-depth) and (b) JN-D (1100 m-depth) during 14-15 January 2006. Error bars indicate the standard deviations.

Figure 6. The day and night vertical distribution of the color of the copepods (in percentage) at stations (a) JN-S (145 m-depth) and (b) JN-D (1100 m-depth) during14-15 January 2006.

Figure 7. Temperature, salinity, fluorescence, pressure and density profile of (a) JN-S and (b) JN-D.

Figure 8. Pictures of (a) pigmented copepod collected in the upper 40 m at JN-S during day sampling, and (b) transparent copepod collected in the upper 40m at JN-S during night sampling.

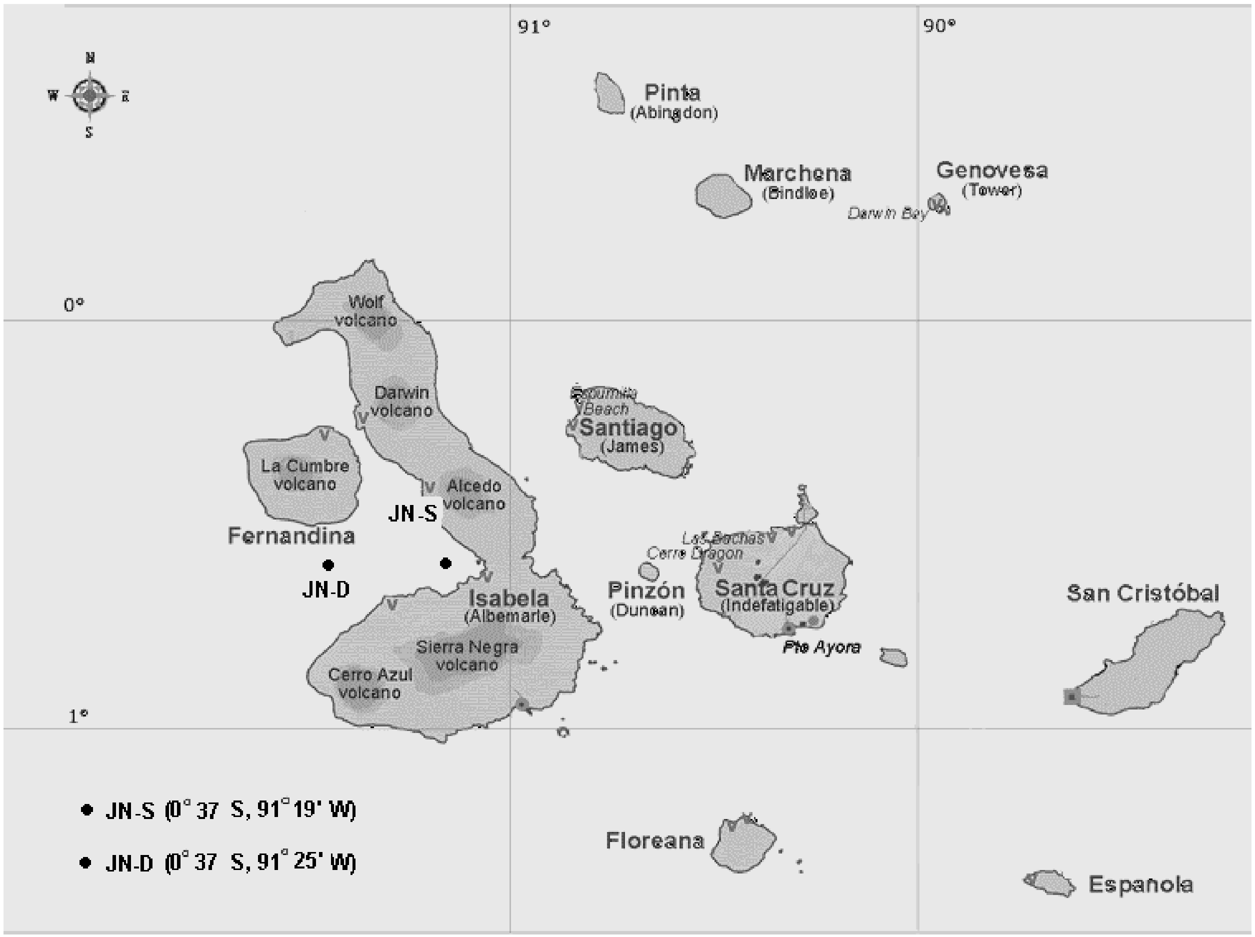
N
W
E
S
91°
90°
Pinta
(Abingdon)
Marchena
(Bindloe)
Genovesa
(Tower)
Darwin Bay
0°
Wolf
volcano
Darwin
volcano
Espumilla
Beach
Santiago
(James)
La Cumbre
volcano
Alcedo
volcano
JN-S
Fernandina
JN-D
Las Bachas
Cerro Dragon
Pinzón
(Duncan)
Santa Cruz
(Indefatigable)
Isabela
(Albemarle)
Sierra Negra
volcano
Cerro Azul
volcano
Pto Ayora
San Cristóbal
1°
● JN-S (0° 37 S, 91° 19' W)
● JN-D (0° 37 S, 91° 25' W)
Floreana
Espanola

Figure 1

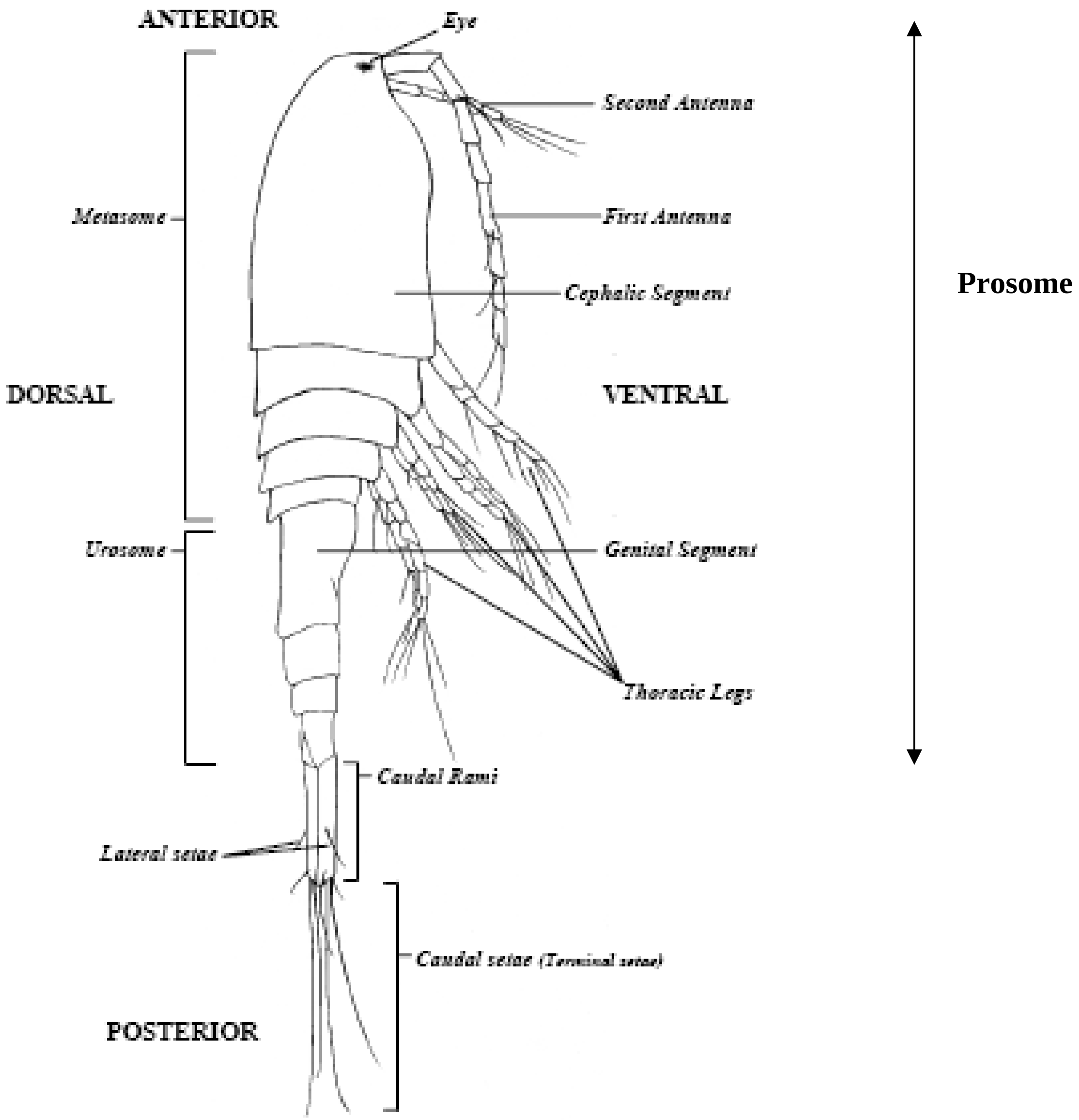
ANTERIOR
Eye
Second Antenna
Metasome
First Antenna
Cephalic Segment
Prosome
DORSAL
VENTRAL
Urosome
Genital Segment
Thoracic Legs
Caudal Rami
Lateral setae
Caudal setae (Terminal setae)
POSTERIOR

Figure 2

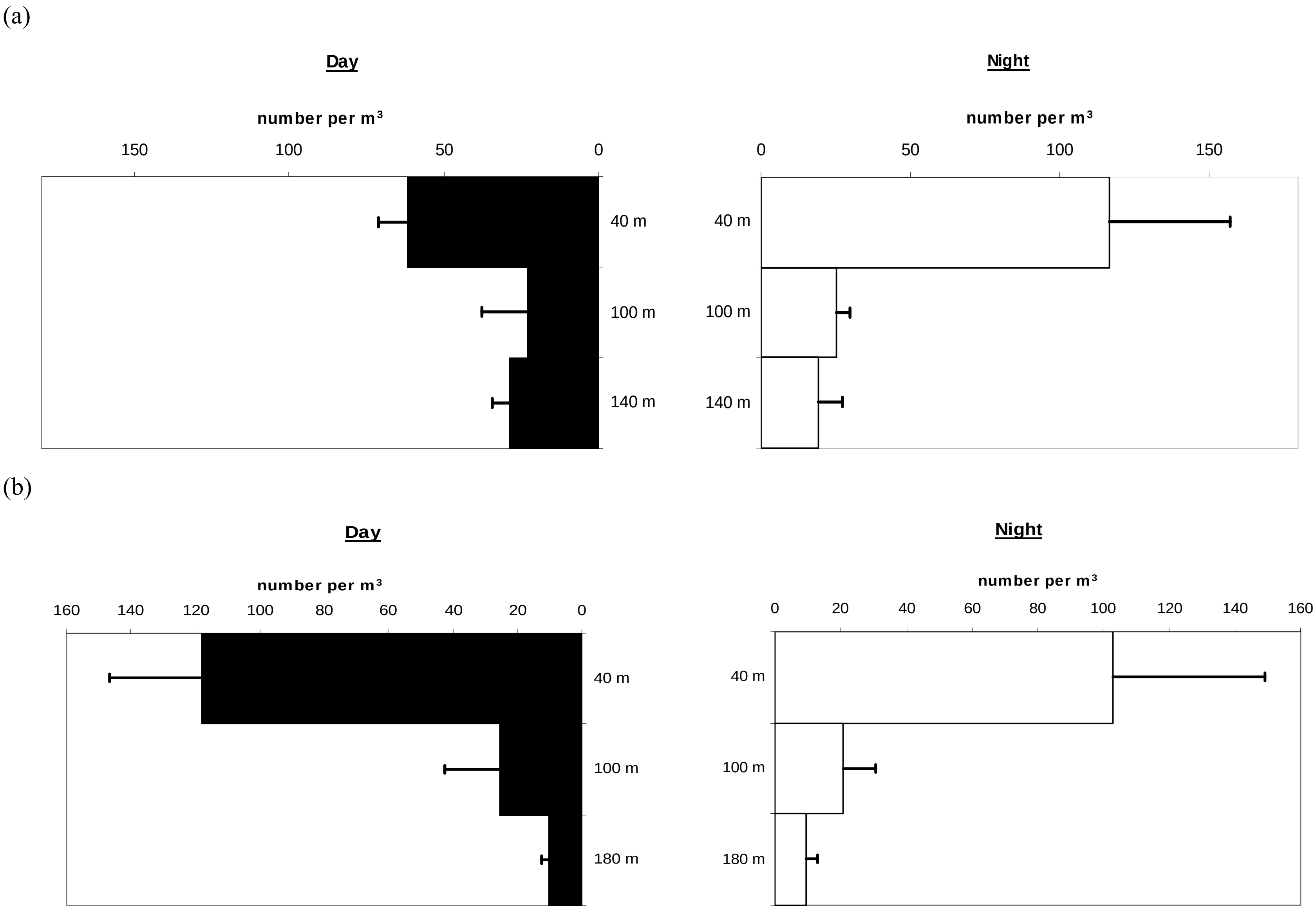
(a)
Day
number per m³
150
100
50
0
40 m
100 m
140 m
Night
number per m³
0
50
100
150
40 m
100 m
140 m
(b)
Day
number per m³
160
140
120
100
80
60
40
20
0
40 m
100 m
180 m
Night
number per m³
0
20
40
60
80
100
120
140
160
40 m
100 m
180 m

Figure 3

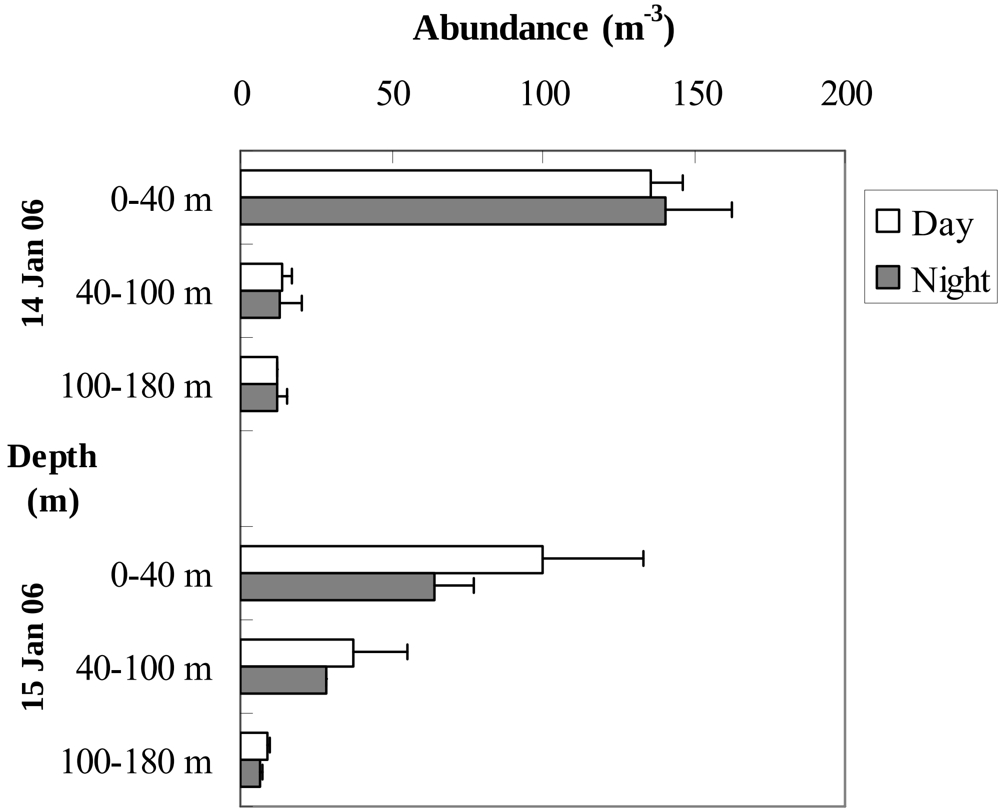
Abundance (m^{-3})
0
50
100
150
200
14 Jan 06
0-40 m
40-100 m
100-180 m
Depth (m)
15 Jan 06
0-40 m
40-100 m
100-180 m
☐ Day
▨ Night

Figure 4

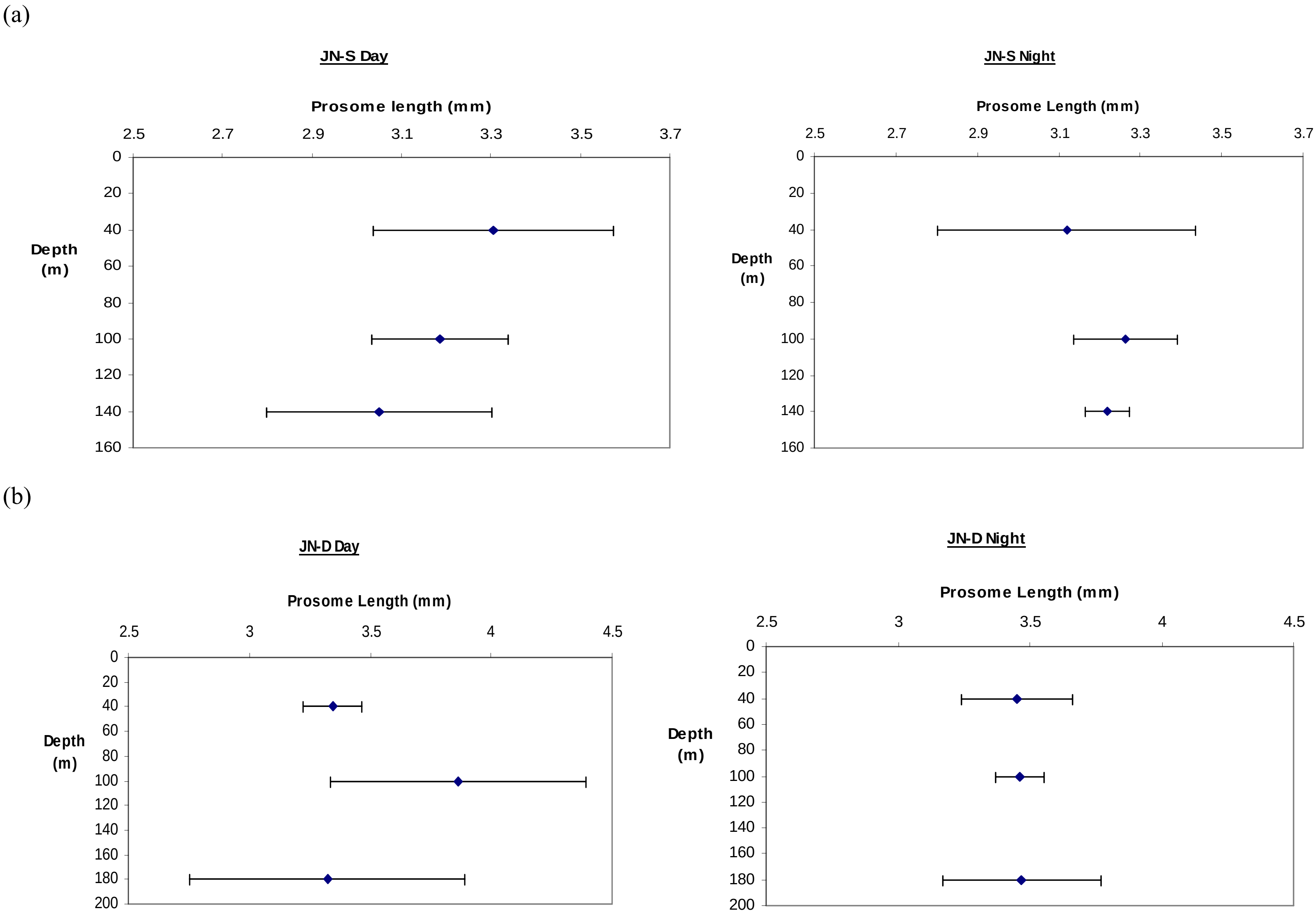
(a)
JN-S Day
Prosome length (mm)
2.5
2.7
2.9
3.1
3.3
3.5
3.7
Depth (m)
0
20
40
60
80
100
120
140
160
JN-S Night
Prosome Length (mm)
2.5
2.7
2.9
3.1
3.3
3.5
3.7
Depth (m)
0
20
40
60
80
100
120
140
160
(b)
JN-D Day
Prosome Length (mm)
2.5
3
3.5
4
4.5
Depth (m)
0
20
40
60
80
100
120
140
160
180
200
JN-D Night
Prosome Length (mm)
2.5
3
3.5
4
4.5
Depth (m)
0
20
40
60
80
100
120
140
160
180
200

Figure 5

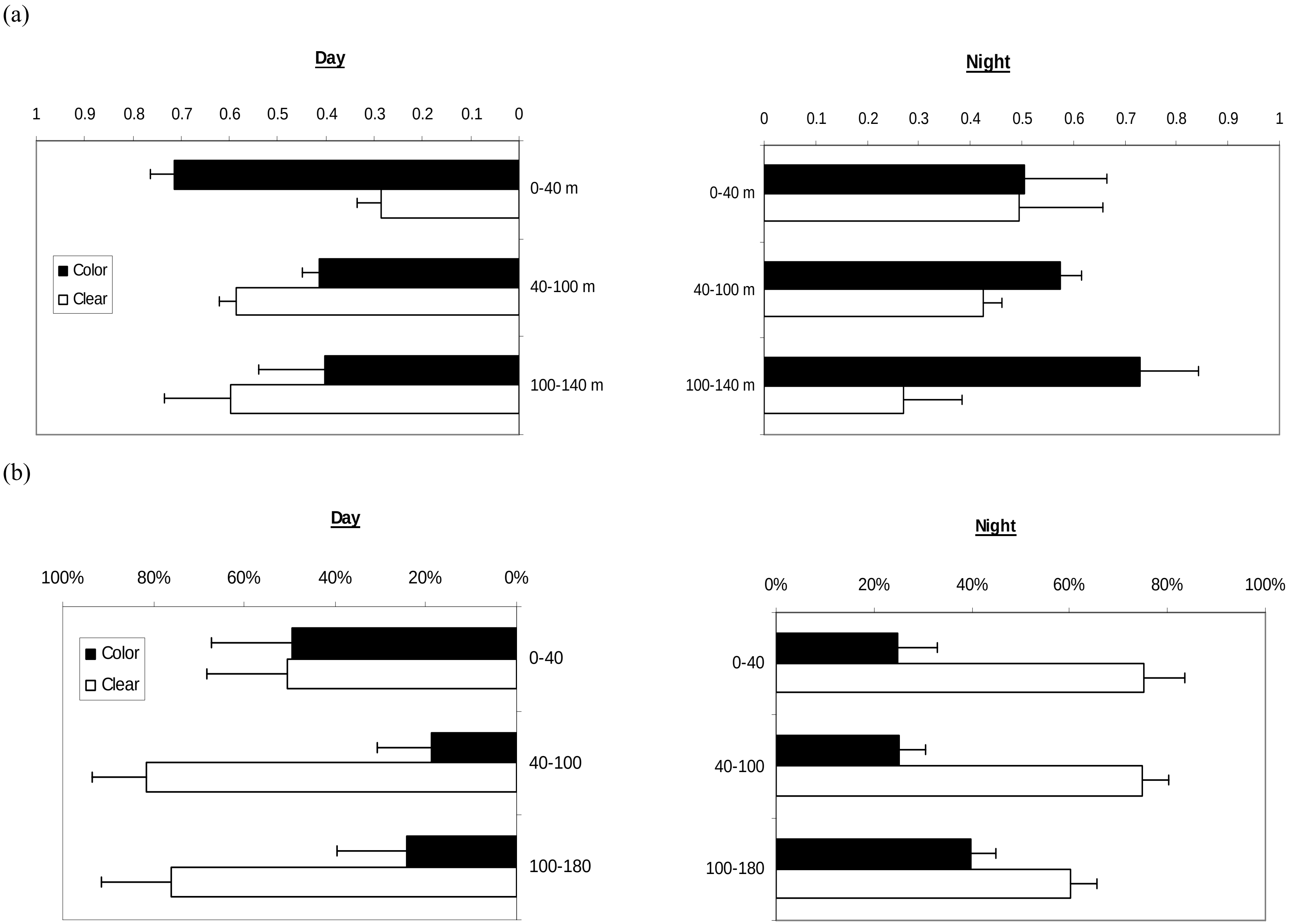
(a)
Day
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0-40 m
40-100 m
100-140 m
■ Color
□ Clear
Night
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0-40 m
40-100 m
100-140 m
(b)
Day
100%
80%
60%
40%
20%
0%
■ Color
□ Clear
0-40
40-100
100-180
Night
0%
20%
40%
60%
80%
100%
0-40
40-100
100-180

Figure 6

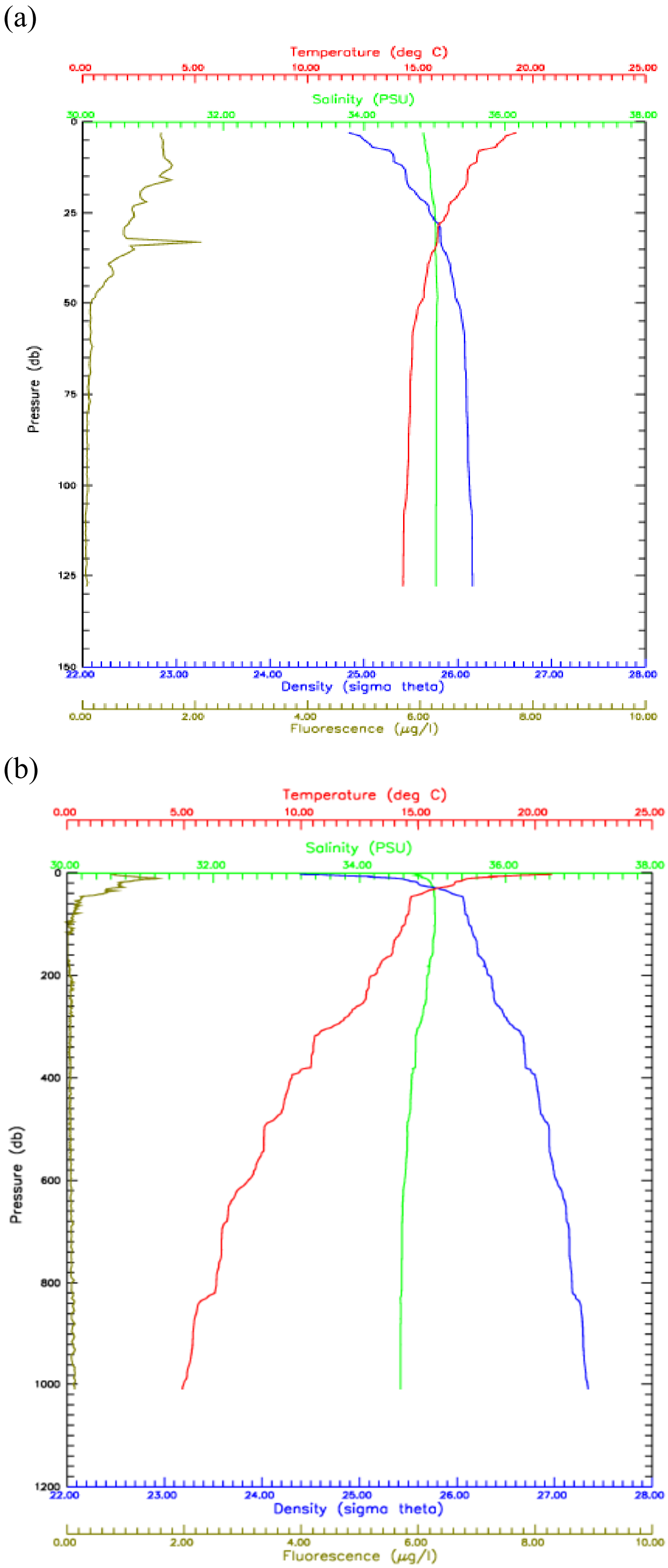
(a)
Temperature (deg C)
0.00
5.00
10.00
15.00
20.00
25.00
Salinity (PSU)
30.00
32.00
34.00
36.00
38.00
Pressure (db)
0
25
50
75
100
125
150
Density (sigma theta)
22.00
23.00
24.00
25.00
26.00
27.00
28.00
Fluorescence (µg/l)
0.00
2.00
4.00
6.00
8.00
10.00
(b)
Temperature (deg C)
0.00
5.00
10.00
15.00
20.00
25.00
Salinity (PSU)
30.00
32.00
34.00
36.00
38.00
Pressure (db)
0
200
400
600
800
1000
1200
Density (sigma theta)
22.00
23.00
24.00
25.00
26.00
27.00
28.00
Fluorescence (µg/l)
0.00
2.00
4.00
6.00
8.00
10.00

Figure 7

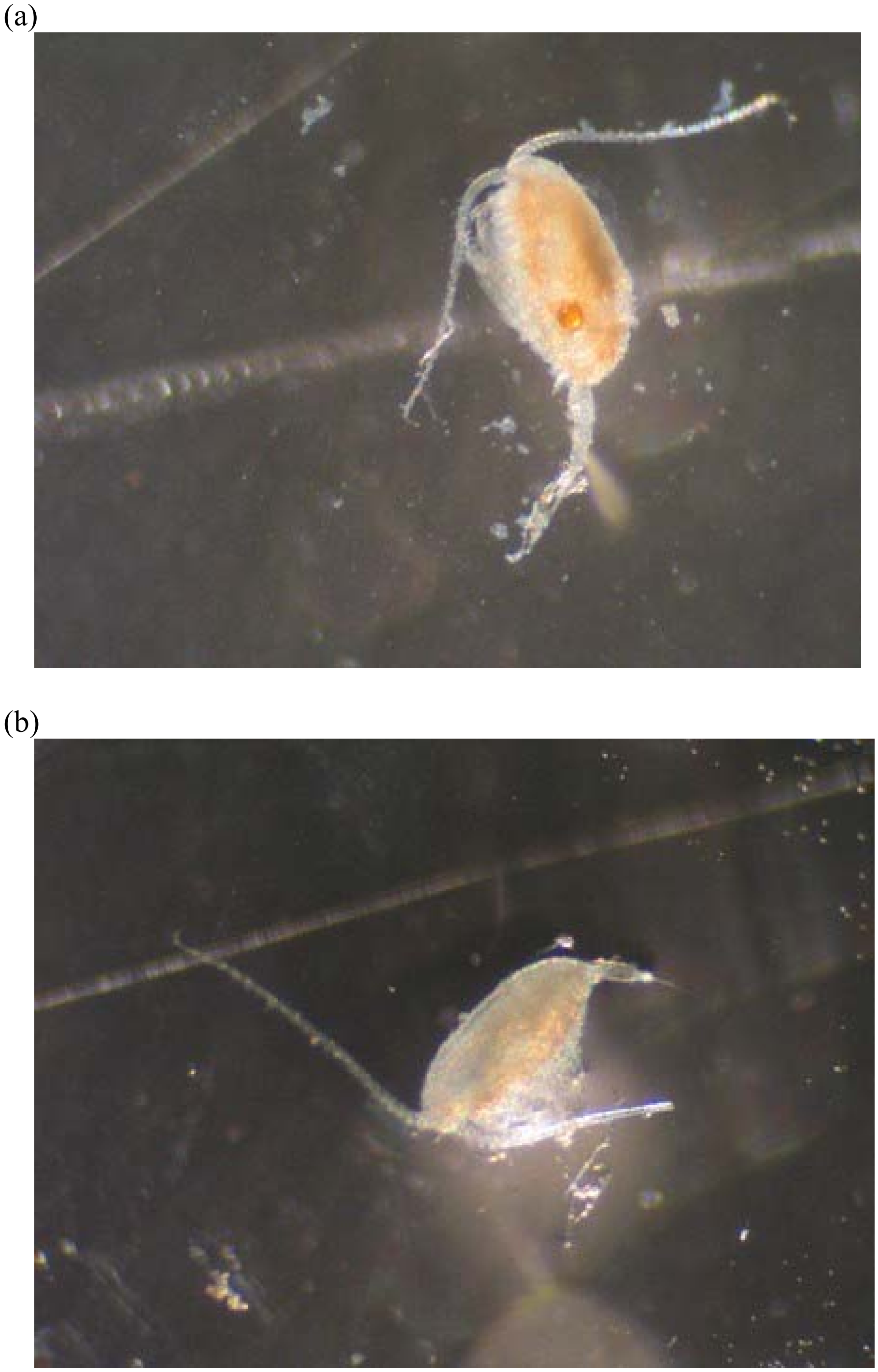

Figure 8