Diel variability in vertical distribution of mesozooplankton populations in a high chlorophyll plume of the Galapagos Archipelago, Ecuador

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Running Head: Vertical distribution of mesozooplankton in the Galapagos Archipelago, Ecuador.

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Non-Technical Summary

Regions of high phytoplankton (primary producers) and zooplankton (secondary producers) growth are essential in supporting growth of juvenile fish and the entire marine food web. The eastern equatorial Pacific in the vicinity of the Galapagos Archipelago supports a tongue of increased productivity up to 7.7 times greater then the surrounding subtropical gyres. While this region of elevated productivity has been well described seaward of the islands, little is known about the archipelago's immediate distribution of plankton populations. This study examined the vertical distribution of secondary producers, specifically mesozooplankton (>300 μm), which both represent and support the unusual regional biota. A high chlorophyll plume to the west of Isabela Island was sampled for mesozooplankton January 2006, utilizing a 1 m diameter Puget Sound closing net (300 μm mesh) from the R/V Thomas G. Thompson. Two different sites were examined, a shallow site (145 m depth) and a deep site (1100 m depth). Vertical sampling was employed during the day and night within different sections of the water column in order to examine whether vertical movement of specific zooplankton groups occurred over a 24 hour period. This movement is known as diel vertical migration (DVM) and should result in larger catches at night in the surface layers. Evidence for normal DVM was found in euphausiid nauplii, though data for euphausiids, chaetognaths, ostracods and others proved inconclusive due to small sample sizes.

Acknowledgements

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Abstract

Regions of elevated primary (phytoplankton) and secondary (zooplankton) productivity are indicative of high levels of fish recruitment and function as a considerable basis of the marine food web. The eastern equatorial Pacific in the vicinity of the Galapagos Archipelago supports a tongue of increased productivity up to 7.7 times greater then the surrounding subtropical gyres. While this region of elevated productivity has been well described seaward of the islands, little is known about the archipelago's immediate distribution of plankton populations. This study examined the vertical distribution of secondary producers, specifically mesozooplankton, which both represent and support the unusual regional biota. A high chlorophyll plume to the west of Isabela Island was sampled for mesozooplankton January 2006, utilizing a 1 m diameter Puget Sound closing net (300 μm mesh) from the R/V Thomas G. Thompson. Semidiurnal depth discreet vertical sampling was employed within two different sites, a shallow site (145 m depth) and a deep site (1100 m depth), in order to examine whether vertical spatial variability occurred indicative of diel vertical migration (DVM). Evidence for normal DVM was found in euphausiid nauplii, though data for euphausiids, chaetognaths, ostracods and others proved inconclusive due to small sample sizes.

Introduction

Regions of high primary and consequent secondary production are essential to high levels of fish recruitment (Feldman 1986; Okey et al. 2004) and instrumental to sustaining the marine food web. The tongue of heightened productivity in the eastern equatorial Pacific is up to 7.7 times greater then the surrounding subtropical gyres that span ~45ºN to 45ºS(Chavez et al. 1996), making it vital to Pacific Basin productivity.

While satellite imagery depicting sea surface color permits observation of the global distribution of primary producers through chlorophyll standing stock, we have no such applications describing secondary producers - the zooplankton - resulting in the need to determine distribution trends via direct measurement. In the case of the Galapagos, preliminary work describing regional zooplankton community composition has been accomplished by Figueroa and Hoefel (unpubl.) across the archipelago. They reported the emergence of divergent patterns regionally separating the western, central and southern zooplankton populations. The region to the west of Isabela Island was characterized as a distinct bioregion with especially high productivity and a zooplankton community composition dominated by 78.7 % copepods (Table 1; Figueroa and Hoefel unpubl.).

In addition to regional horizontal variability in zooplankton communities, vertical variability is often found in zooplankton through diel vertical migrations (DVM) to and from the euphotic zone. DVM is thought to maximize energy gain and reduce risks of daylight predation from planktivorous nekton (De Robertis et al. 2000; Rollwagen Bollens and Landry 2000; Strom 2002; Tarling et al. 2002) in turn affecting a significant portion of carbon flux from the euphotic zone (Richardson et al. 2004; Roman et al. 1995; Pearre 2003). Timing of vertical migrations has been shown to coincide with zooplankton size where larger animals ascend 30 minutes later

and descend 45 minutes earlier than smaller bodied organisms (Fig. 1), suggesting that larger organisms are more conspicuous to planktivorous predators (De Robertis et al. 2000). Increased diel vertical migrations have also been attributed to faster swimming speeds of large zooplankton in comparison to smaller congeners, and to physical parameters including increased light levels and the depth of the mixed layer (Longhurst 1976). Other factors controlling distance of DVM are site-specific topographical relief and intensity of upwelling currents. In areas of shelf breaks, migration can increase due to related upwelling enhanced primary productivity and depth of habitat (Genin 2004). Whereas vertical zooplankton dispersal has been well described for the central and eastern equatorial Pacific through the Joint Global Ocean Flux Study (JGOFS) (Roman et al. 1995), little information is available to describe vertical distribution of zooplankton in the immediate vicinity of the Galapagos Archipelago.

The main objective of this study was to investigate the poorly defined diel vertical distribution of mesozooplankton (>300μm) in the Galapagos Archipelago across different depth habitats (Fig. 2). Vertical distribution of copepods was only given cursory examination as Natalie Tsui shared in all samples and described size (by prosome length) and pigment dependant distribution. Beyond the preliminary work already mentioned that examined species composition of zooplankton around the islands (Figueroa and Hoefel unpubl.), little is known about their in situ behavior. Diel migration was inferred from vertical distributions, determined by replicate semi-diurnal net sampling (300μm mesh) in both shallow (145 m) and deep (1100 m) water habitats. The sampling area was to the west of Isabela Island in a productive region (Fig. 3) where species composition at the two sampling sites was expected to be similar based on previously mentioned findings (Figueroa and Hoefel unpubl.); differences in patterns of

distribution would therefore largely be attributable to variation in size of zooplankters and depth of habitat.

Methods

The study area was in the high chlorophyll plume to the west of Isabela Island: a 145 m deep site (JN-S) and an 1100 m deep site (JN-D) were sampled from the R/V Thomas G. Thompson (Table 2; Fig. 3) on January 14 and 15, 2006. Target times for stations were chosen to best capture zooplankton within depth extremes during non-migrational periods during the day and at night; actual times on station are recorded in Table 2.

To establish diel variability in vertical distribution of mesozooplankton populations, depth discrete vertical net sampling was used to profile the top of the water column. Distribution was established through replicate day and night hauls employing a 1 m diameter Puget Sound closing net (Miller et al. 1984) rigged with 300 μm mesh. Descent rates were 20-30 m min^{-1} and the ascent rate was 20 m min^{-1}. A maximum sampling depth of 180 m was possible; however at the shallow station the maximum sampling depth was designated as 140 m as the water depth at the station was 145 m.

Conductivity, temperature and depth (CTD) data were first collected to identify the location of the thermocline and chlorophyll *a* maximum via fluorescence profiles. Three depth bins were then designated upon the initial cast per station to isolate the chlorophyll *a* maximum and remained unchanged throughout the following samples (Fig. 4B; Fig. 5B). For the shallow station the three depth strata were 0-40 m, 40-100 m, and 100-140 m. The deep station strata were 0-40 m, 40-100 m, and 100-180 m.

All hauls were evenly divided twice with a Folsom Plankton Splitter and distributed amongst collaborators Natalie Tsui, Diego Figueroa and Christian Naranjo. Bio-volume of all samples was established through displacement volumes: the differences in volume of the parcel of water were noted before and after zooplankton were removed (Harris et al. 2000), as measured using a 250 ml graduated cylinder. Mesozooplankton samples were separated from seawater by filtration through a 120 μm mesh sieve. For graphical comparisons of biovolume as a function of depth, biovolumes were multiplied by the number of samples after splitting then divided by the volume of the related depth bin to account for the varying size of the depth strata.

Samples were fixed in 3.7% formaldehyde (final concentration) to facilitate enumeration. Subsequently, each sample was gently mixed before removing a 5 ml subsample to examine under a dissecting microscope (20-100x magnification). General composition of samples from each depth bin was established by frequency of organisms enumerated through 50 counts. Individuals were identified by class and were not species specific.

Results

When examining totals compiled over the entire sampling depth for each station, overall zooplankton abundances expressed through biovolumes (ml m^{-3}) were higher at night than during the day in both shallow-water (JN-S; Fig. 6B) and deep-water (JN-D; Fig. 6A). Station JN-S bio-volume was 0.55 ± 0.12 ml m^{-3} greater at night and JN-D 0.42 ± 0.15 ml m^{-3} greater. In addition, shallow-water biovolumes were greater than deep-water biovolumes both day and night measuring 0.64 ± 0.14 ml m^{-3} and 0.51 ± 0.15 ml m^{-3}, respectively. However, when semidiurnal station biovolume was expressed as a function of depth for each individual depth bin, only the

shallow-water deep depth bin showed significant difference (0.80 ± 0.36 ml m^{-3}) in biovolume between day and night abundances (Fig. 4A; Fig. 5A).

Individual classes within the mesozooplankton population were found to display divergent migrational patterns upon examination of community composition data across depth habitats. In all cases, copepods dominated the community composition and did not display evident patterns of migration (Fig. 7 A, B; Fig. 8 A, B): certainly this category was too broad to distinguish discernable DVM and was investigated in further detail by Natalie Tsui (2006). In some classes, organisms were present in the upper layers in greater numbers during daylight hours than at night possibly indicative of reverse DVM: examples are chaetognaths at the deep station (Fig. 9 A, B) and jellies at the shallow station (Fig. 10 A, B). Increased euphausiid nauplii abundances in surface waters at night at JN-S were consistent with normal DVM. Euphausiids were found only at night, regardless of depth, at both stations (Fig. 9 A, B; Fig. 10 A, B). Ostracod numbers also increased during night at both stations, while Cladocera increased in the surface layer at night in the deep station, but were not present in significant numbers at the shallow station (Fig. 9 A, B; Fig. 10 A, B).

Discussion

Percent community composition of mesozooplankton was comparable with previous unpublished work of Figueroa and Hoefel at the deep station, in particular in copepod, euphausiid and chaetognath abundance (Table 1; Fig. 7 A, B). Variations were present however, ctenophores were not found in any sample and the shallow station exhibited considerably distinct community composition with much less copepod and increased euphausiids (Table 1; Fig. 8 A, B).

After compiling total biovolume for each station, higher biovolumes were found at both sites at night than during the day (Fig. 6 A, B). Much of this difference at the shallow station was attributable to the greater biovolume at night than day in the deepest depth bin (Fig. 5 A). One possible explanation of high nightly biovolume is that increased net avoidance was taking place during daylight hours by the mesozooplankton. Active swimming by mesozooplankton to avoid capture has been argued as capable of introducing considerable bias (Harris et al. 2000). A primary variable by which euphausiid could avoid capture by net, speed of towing is named a main component (Mauchline 1980). Possibly, ascent speed for the net tow at 20 m min^{-1} was too slow, allowing mesozooplankton time enough to swim away from the oncoming net. Euphausiids in particular are thought to exhibit this behavior particularly due to large eyes enhancing their vision; this may explain their detection only at night.

Another possible explanation has to do with the habitat depth, which could also contribute to understanding the increased abundances in the shallow station compared to the deep station. Mesozooplankton could have been exhibiting greater degrees of DVM in the deeper habitat accounting for reduced biomass over the study area if they were migrating beyond the sampling depth. For instance, some coastal species of euphausiid are reported as having total vertical ranges up to 500 m, a distance much greater than our maximum sampling depth with average day depths reported to range between 10-300 m depending on species (Mauchline 1980). It is possible that mesozooplankton were migrating beyond the sampling depth in the shallow station as well, though it is unlikely as the water column was sampled to within 5 m of the seabed and zooplankters are not wholly associated with the seafloor.

An additional means of increasing the zooplankton population would be to increase a primary food source, the phytoplankton. Phytoplankton standing stock visible by chlorophyll *a*

seacolor in a SeaWIFS image from the January study suggests increased chlorophyll *a* to the west at JN-D (Fig. 3). However, fluorescence data from the CTD casts does not show noteworthy increases in chlorophyll *a* at either station beyond the first few meters at JN-S (Fig. 4 B, 5 B). Neither of these points supports significantly increased productivity in the eastward station attributable for the overall increase in mesozooplankton biovolume of the shallow station.

Vertical distributions of mesozooplankton populations were consistent with typical vertical migration only in a few cases examining behavior within classes and not across the zooplankton community as a whole. The most compelling of these were the nauplii at the shallow station JN-S (discussed below). Other possible examples include ostracods and euphausiids, but the small sample sizes in the first case, and the likelihood of net avoidance or migrational ranges beyond our sampling depths in the latter case, limit definite conclusions. Reverse vertical migration appeared to take place in some of the gelatinous organisms, the chaetognaths and jellies but numbers are too small to be conclusive (Fig. 9 A, B; Fig. 10 A, B).

As noted above, the most distinctive patterns of DVM were displayed by the euphausiid nauplii: their numbers increased during the night in both depth habitats. At station JN-S, nauplii not only increased in both the surface and mid-water strata at night but were no longer present in the deep stratum, presumably because they had migrated upward (Fig. 10 A, B). The situation was less clear at JN-D, but the increase in the depth stratum at night could imply vertical migration from below the sampling depth. That the strongest evidence for normal vertical migration was seen at the shallow station and is consistent with Natalie Tsui's (2006) work on copepods: she too found pronounced evidence of DVM only at JN-S (Fig. 11). Evidence for normal DVM in euphausiid larva has been demonstrated in Sagami Bay and Suruga Bay off of

Japan (Hirota et al. 1984) and for copepod nauplii in the equatorial Pacific (Rollwagen Bollens and Landry 2000).

Conclusion

Mesozooplankton community composition was compiled for the high chlorophyll plume west of Isabela Island, along with information on diel variability in their vertical distribution. Similarities with previous work on community composition (Figueroa and Hoefel unpubl.) were found to coincide with the deep station JN-D. Differences were evident when compared with JN-S which exhibited considerably more euphausiid and less copepod. No ctenophores were found in either station.

Significant increases in biovolume occurred at night in comparison with the day at both of the study sites and are suspected to be due to net avoidance by mesozooplankton as they swam to avoid capture. Euphausiids were collected only during the night thus vertical movement cannot be inferred. It is possible that they were present during the day at both stations and were effectively exhibiting net avoidance or that the euphausiid's vertical range was greater than our sampling depth.

Strong evidence for normal DVM was found only in euphausiid nauplii, all other evidence, including evidence of reverse DVM, was inconclusive due to small sample sizes. Further, differences in naupliar DVM were found to exist between stations as no nauplii were present at night in the shallow station bottom depth bin and nauplii increased in the deep station bottom depth bin. Possibly nauplii were migrating up from below our sampling depth at night in the deep station.

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Tables

Table 1: Composition of the zooplankton assemblage on the west side of Isabela Island. Sample percentages correspond to a single haul collected in February 2005 near the north end of the island (Figueroa and Hoefel unpubl.).

Organisms	Percentage
Copepods	78.70%
Ctenophores	8.20%
Chaetognaths	3.80%
Euphausiids	2.90%
Ostracods	1.50%
Others	4.80%

Table 2: Station locations, water depth and depth bins.

Station:	Position:	Date:	Sampling Times: (local)	Water Depth: (m)	Surface Strata: (m)	Mid-water Strata: (m)	Deep Strata: (m)
JN-S	0º 37'S 91º 19'W	1/14/06	1259-1416	145	0-40	40-100	100-140
		1/14/06 - 1/15/06	2348-0042				
		1/15/06	1017-1101				
		1/15/06	2249-2331				
JN-D	0º 37'S 91º 25'W	1/14/06	1026-1116	1100	0-40	40-100	100-180
		1/15/06	2106-2158				
		1/15/06	0838-0920				
		1/15/06	2107-2152				

Figure legends

Figure 1: Dawn and dusk migrations of euphausiids at 50 m depth, over one hour time periods. Lines separate class sizes. (A) Euphausiid abundance during dusk ascent. (B) Euphausiid abundance during dawn ascent (from De Robertis et al. 2000).

Figure 2: Map of the eastern equatorial Pacific with the Galapagos Archipelago, Ecuador and an inset of the northwestern coast of South America (modified from, Cousteau and Diolé 1973). Station numbers are shown in the bay between Isabela and Fernandina Islands. JN-S is in 145 m of water and JN-D in 1100 m of water.

Figure 3: SeaWIFS map modified to depict location of station sites in the western vicinity of Isabela Island in a picture depicting sea surface color dependant on chlorophyll concentration. Colors indicate productivity, orange represents higher values and blue represents lower values. Black is shown in areas of increased cloud cover except where outlines enclose island masses. Image was collected on 17 January 2006 from 20:10:00 UT through 20:15:00 UT, two days after final zooplankton samples were collected due to cloud cover shrouding image on previous days. Modified from USA NASA government web site. http://oceancolor.gsfc.nasa.gov/cgi/tiles.pl?sub=region_timeseries_table&day=17Jan2006&num=6&rgn=GalapagosIs

Figure 4: Deep water station (JN-D, 1100 m) with a maximum sampling depth of 180 m. (A) Biovolume averages per m^3 for all three depth bins during day and night. Error bars represent standard error values. (B) Fluorescence data profile from initial CTD cast for JN-D taken 14 January 2006.

Figure 5: Shallow water station (JN-S, 145 m) with a maximum sampling depth of 140 m. (A) Biovolume averages per m^3 for all three depth bins during day and night. Error bars represent standard error values. (B) Fluorescence data profile from initial CTD cast for JN-S taken on 14 January 2006.

Figure 6: Biovolume averages per m^3 from all three depth bins compiled for the entire sampling depth for each station during the day and night. Error bars represent standard error values. Note the different depth scales. Diel biovolume averages per m^3 for (A) JN-D and (B) JN-S.

Figure 7: Percent of mesozooplankton groups for each depth bin at the deep station (JN-D, 1100 m). Average numbers are shown inside percentage bars, enumerated from random 5 ml subsamples and 50 counts. Vertical distribution of mesozooplankton groups shown during the day (A) and night (B).

Figure 8: Percent of mesozooplankton groups for each depth bin at the shallow station (JN-S, 145 m). Average numbers are shown inside percentage bars, enumerated from random 5 ml subsamples and 50 counts. Vertical distribution of mesozooplankton groups shown during the day (A) and night (B).

Figure 9: Percent of non-copepod zooplankton groups for each depth bin at the deep station (JN-D, 1100 m). Average numbers are shown inside percentage bars, enumerated from random 5 ml subsamples and 50 counts. Vertical distribution of non-copepod mesozooplankton groups during the day (A) and night (B).

Figure 10: Percent of non-copepod zooplankton groups for each depth bin at the shallow station (JN-S, 145 m). Average numbers are shown inside percentage bars, enumerated from

random 5 ml subsamples and 50 counts. Vertical distribution of non-copepod mesozooplankton groups shown during the day (A) and night (B).

Figure 11: JN-S, shallow water station (145 m) depicting vertical distribution of individual copepods per m^3 within each depth bin. Error bars represent standard error. Note that here black is shown for the day and white at night. Copepods are shown during the day (A) and night (B) (modified from Tsui 2006).

Figures

Figure 1

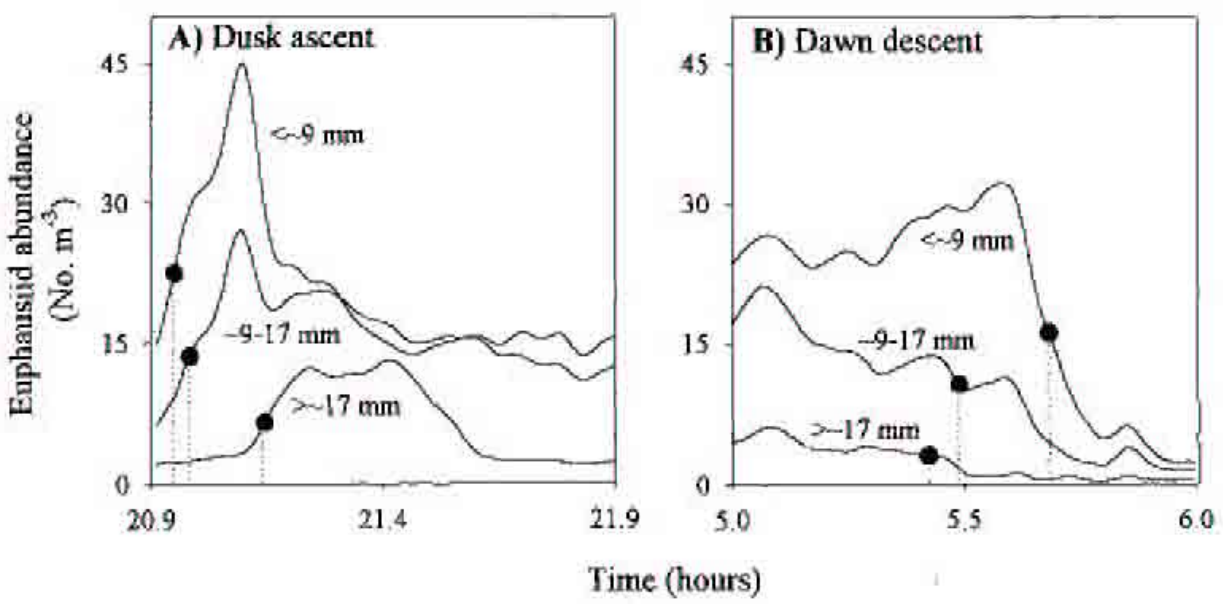
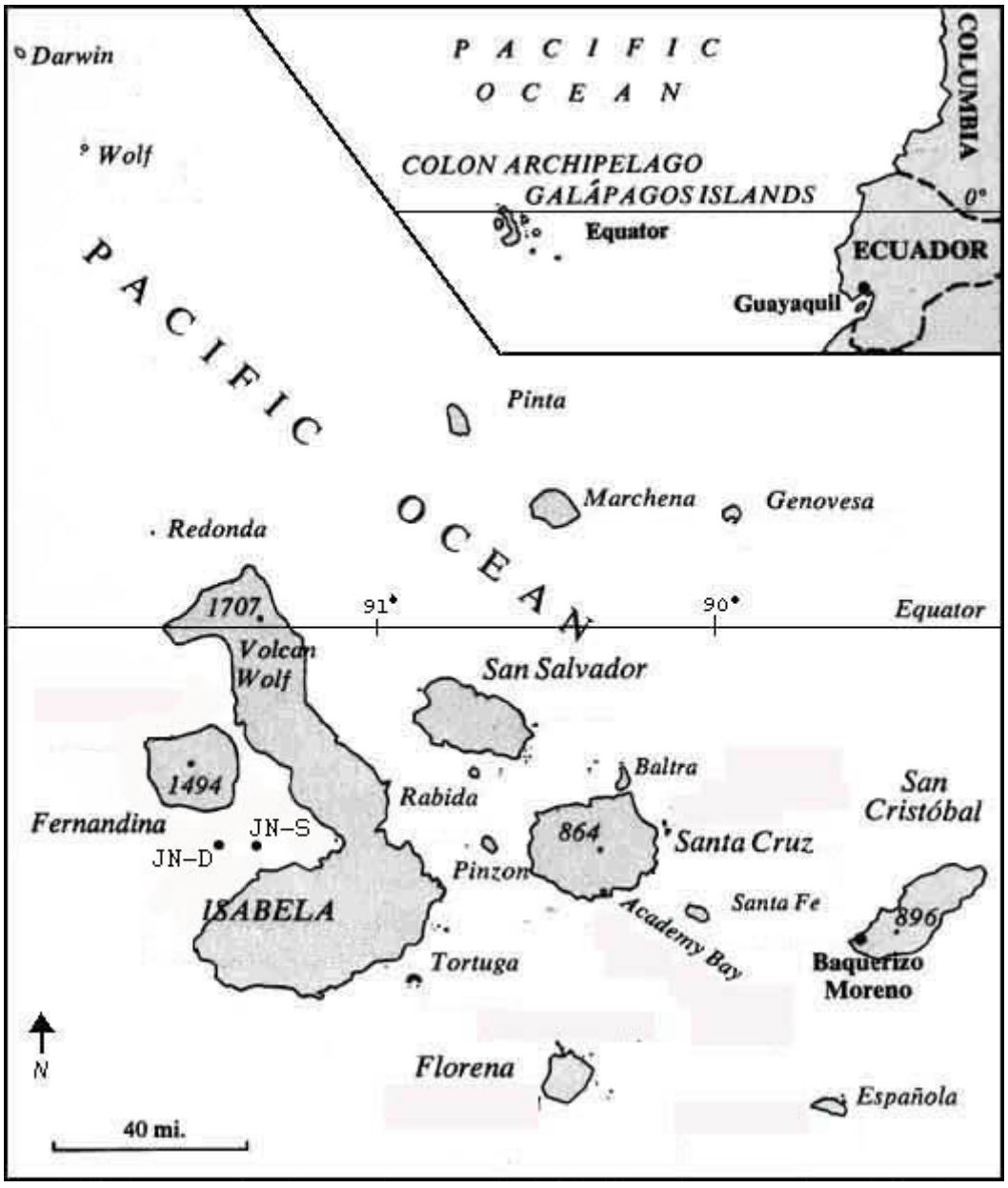


Figure 2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Wolf
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PACIFIC
Pinta
Marchena
Genovesa
Redonda
OCEAN
1707
91°
90°
Equator
Volcan
Wolf
San Salvador
1494
Baltra
Rabida
San
Cristóbal
Fernandina
JN-S
JN-D
864
Santa Cruz
Pinzon
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Baquerizo
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Figure 3

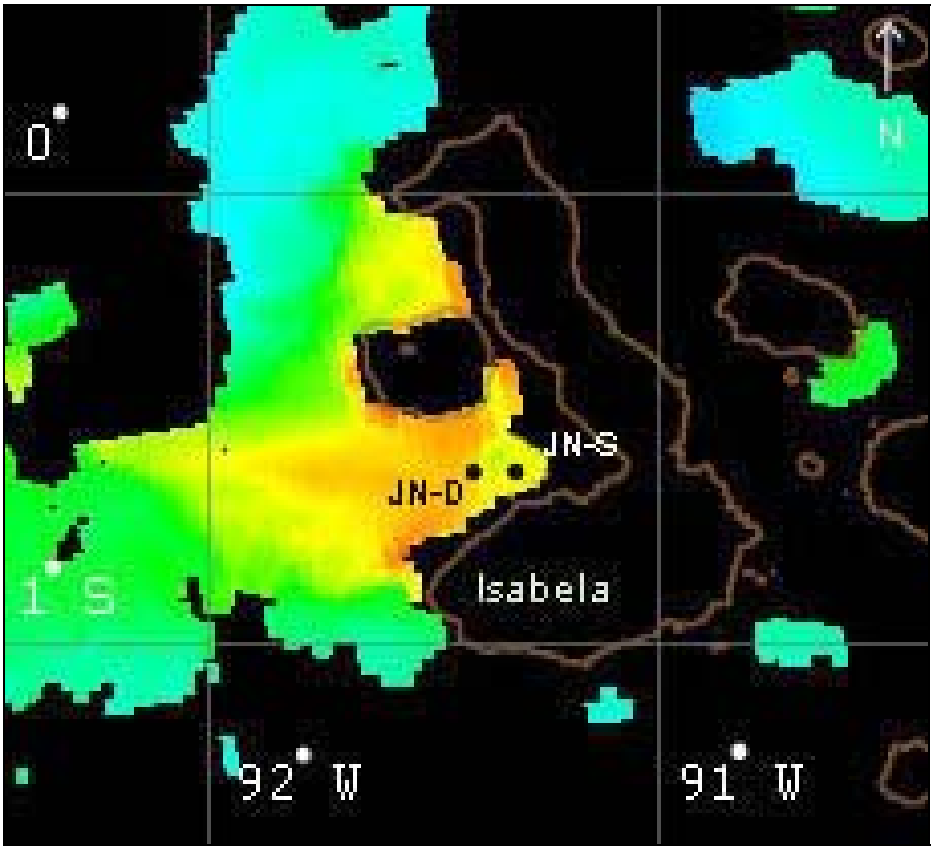


Figure 4

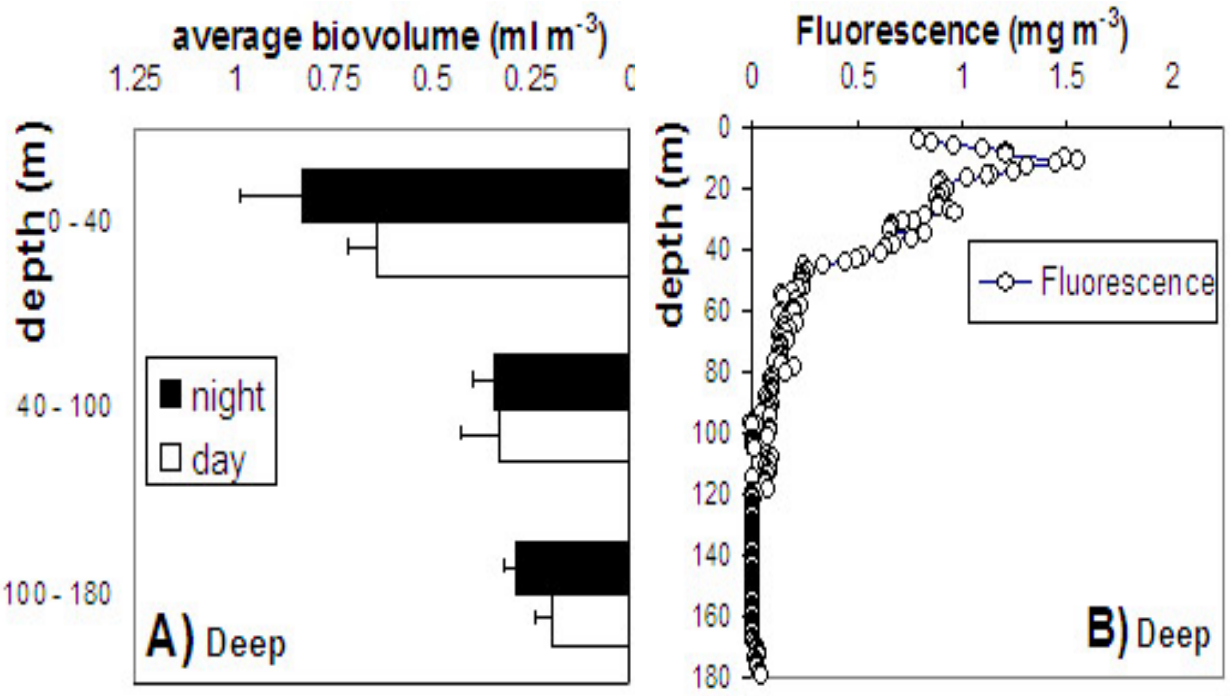

average biovolume (ml m-3)
1.25
1
0.75
0.5
0.25
depth (m)
0 - 40
40 - 100
100 - 180
night
day
A) Deep
Fluorescence (mg m-3)
0
0.5
1
1.5
2
depth (m)
0
20
40
60
80
100
120
140
160
180
Fluorescence
B) Deep

Figure 5

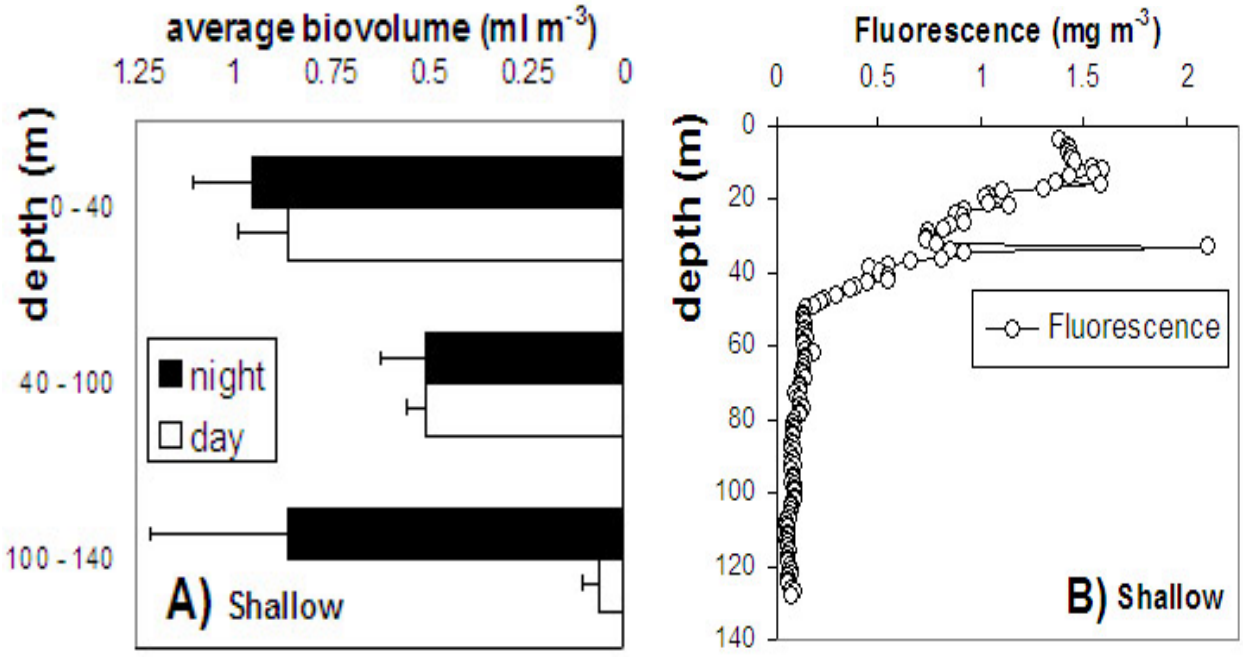

average biovolume (ml m-3)
1.25
1
0.75
0.5
0.25
0
depth (m)
0 - 40
40 - 100
100 - 140
night
day
A) Shallow
Fluorescence (mg m-3)
0
0.5
1
1.5
2
depth (m)
0
20
40
60
80
100
120
140
Fluorescence
B) Shallow

Figure 6

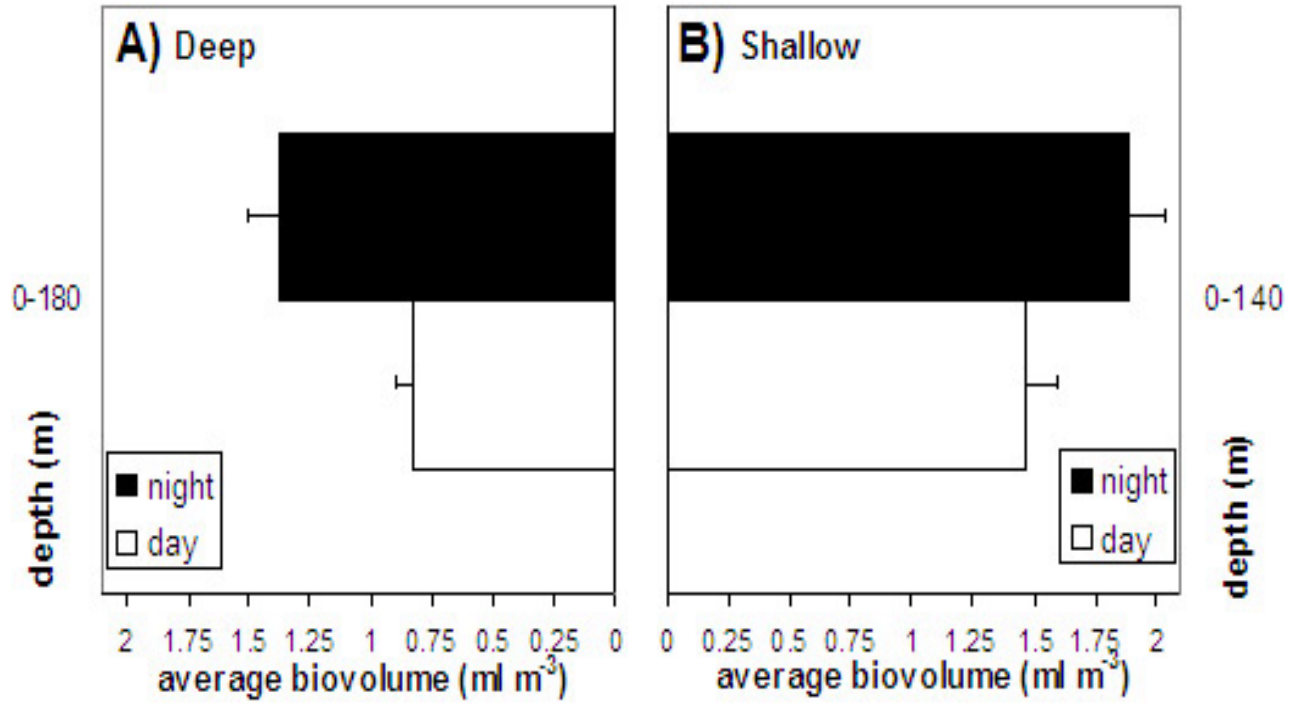

A) Deep
B) Shallow
0-180
0-140
depth (m)
depth (m)
night
day
night
day
2 1.75 1.5 1.25 1 0.75 0.5 0.25 0
0 0.25 0.5 0.75 1 1.25 1.5 1.75 2
average biovolume (ml m-3)
average biovolume (ml m-3)

Figure 7

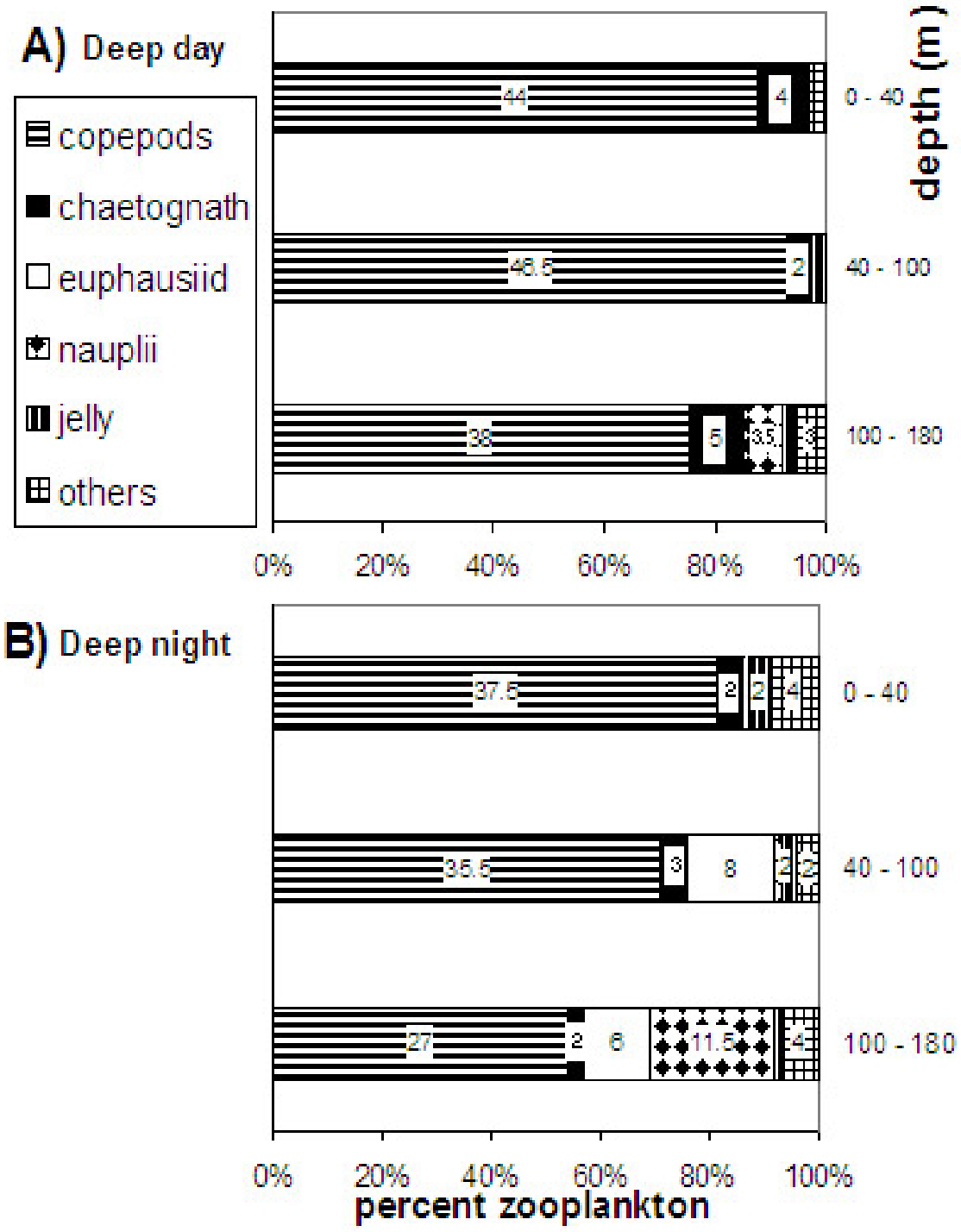

A) Deep day
copepods
chaetognath
euphausiid
nauplii
jelly
others
44
4
46.5
2
38
5
3.5
3
0 - 40
40 - 100
100 - 180
depth (m)
0%
20%
40%
60%
80%
100%
B) Deep night
37.5
2
2
4
36.5
3
8
2
2
27
2
6
11.5
4
0 - 40
40 - 100
100 - 180
0%
20%
40%
60%
80%
100%
percent zooplankton

Figure 8

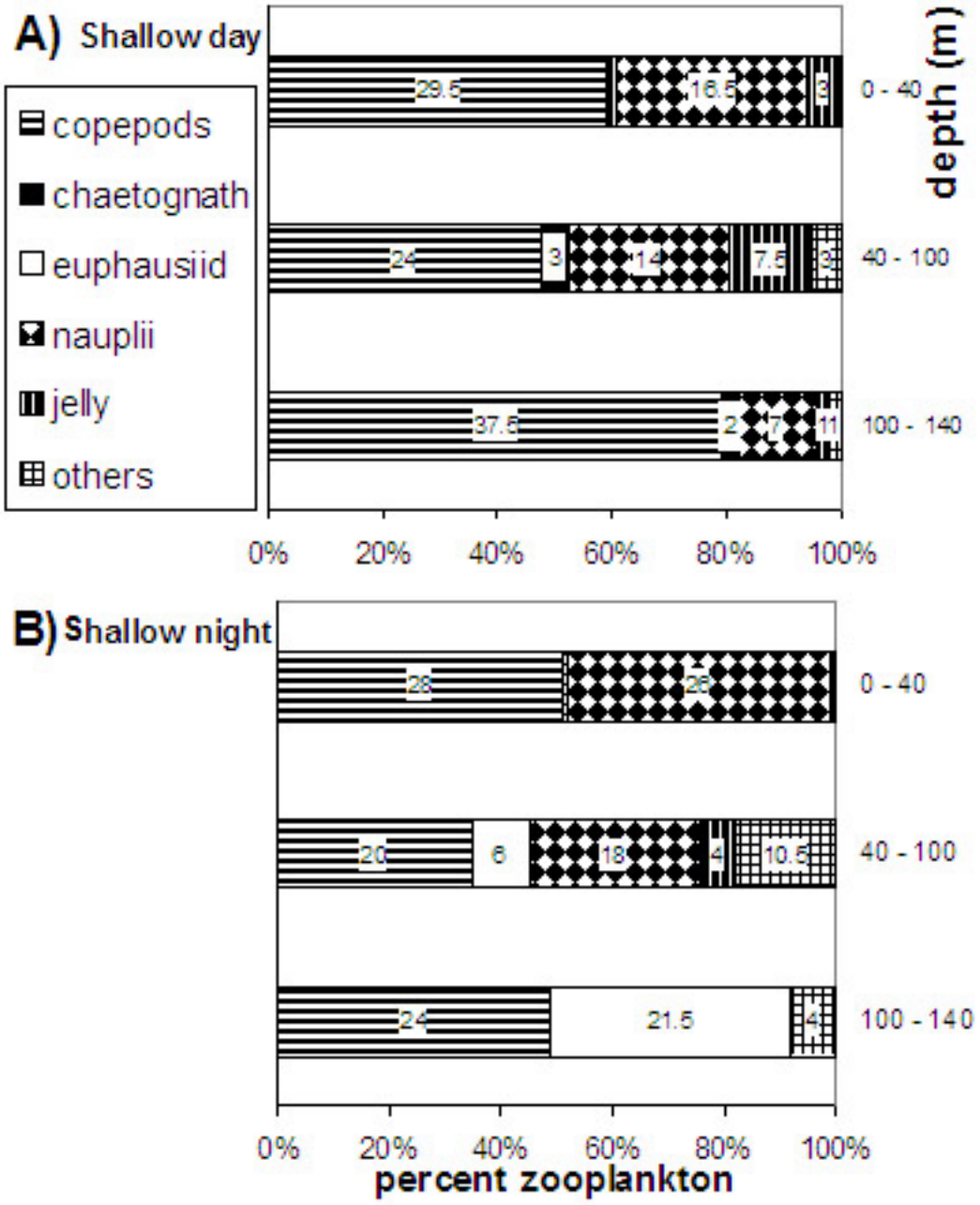

A) Shallow day
copepods
chaetognath
euphausiid
nauplii
jelly
others
29.5
16.5
3
24
3
14
7.5
3
37.5
2
7
11
0 - 40
40 - 100
100 - 140
depth (m)
0%
20%
40%
60%
80%
100%
B) Shallow night
28
26
20
6
18
4
10.5
24
21.5
4
0 - 40
40 - 100
100 - 140
0%
20%
40%
60%
80%
100%
percent zooplankton

Figure 9

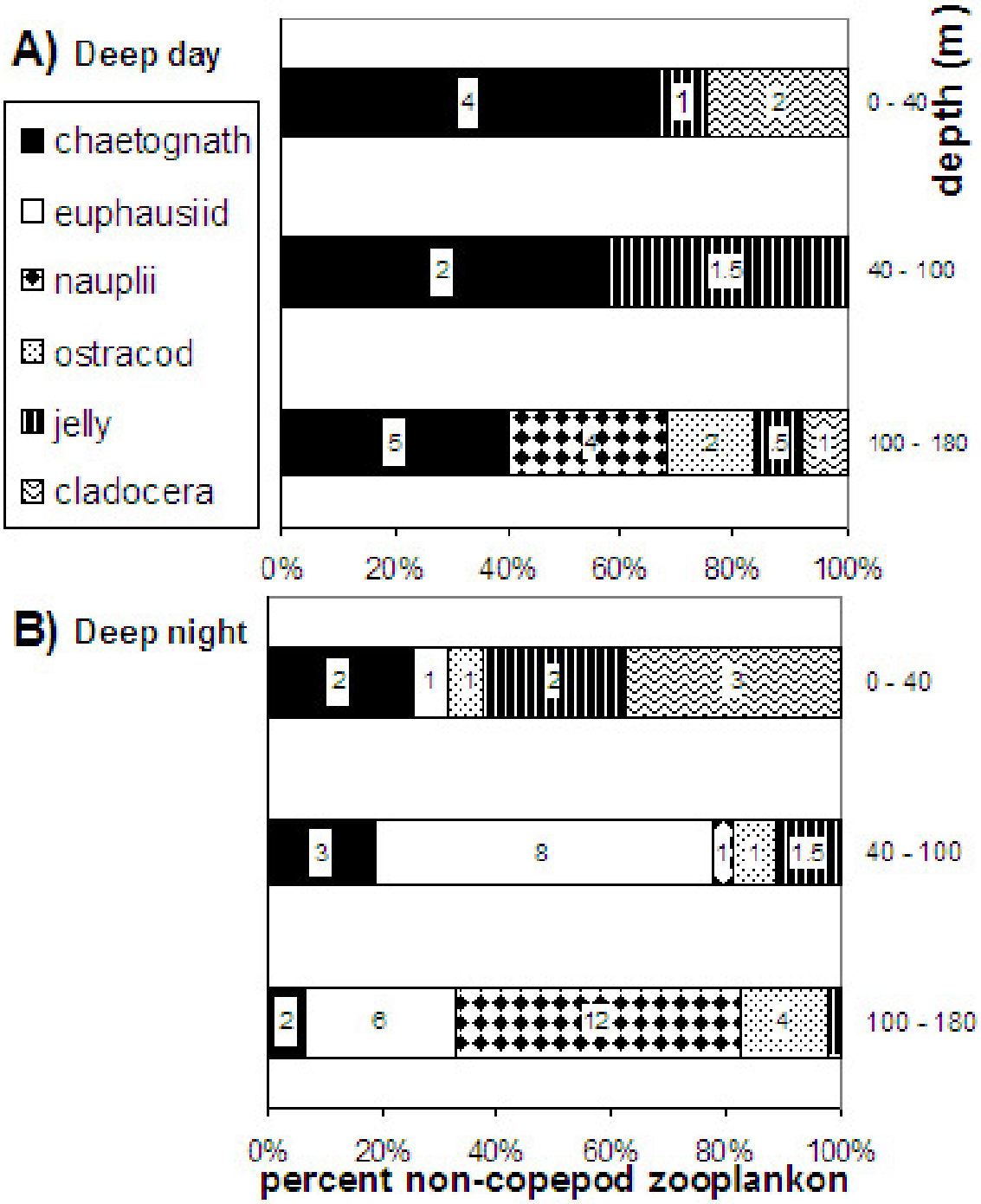

A) Deep day
chaetognath
euphausiid
nauplii
ostracod
jelly
cladocera
4
1
2
0 - 40
2
1.5
40 - 100
5
4
2
.5
1
100 - 180
depth (m)
0%
20%
40%
60%
80%
100%
B) Deep night
2
1
1
2
3
0 - 40
3
8
1
1
1.5
40 - 100
2
8
12
4
100 - 180
0%
20%
40%
60%
80%
100%
percent non-copepod zooplankon

Figure 10

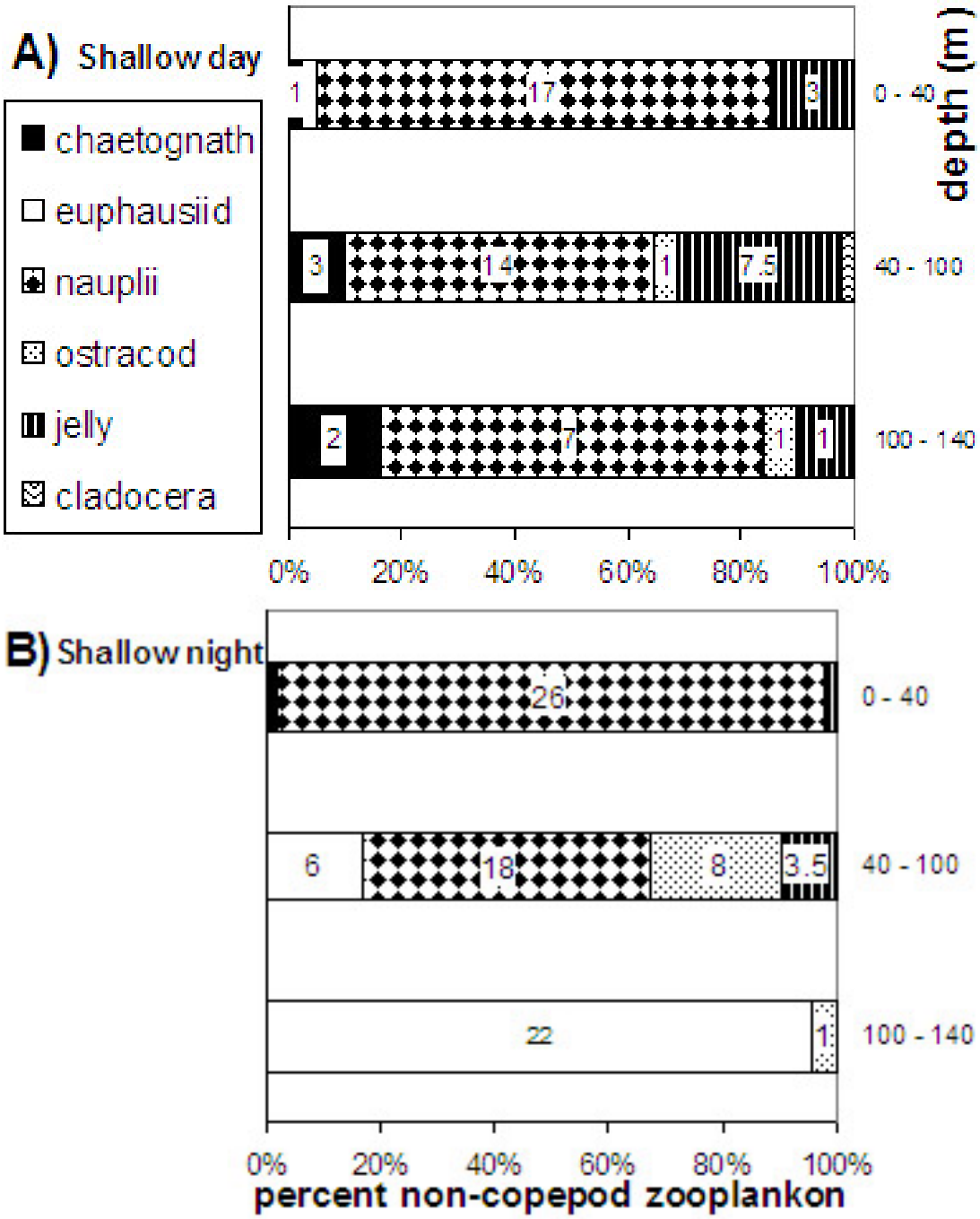
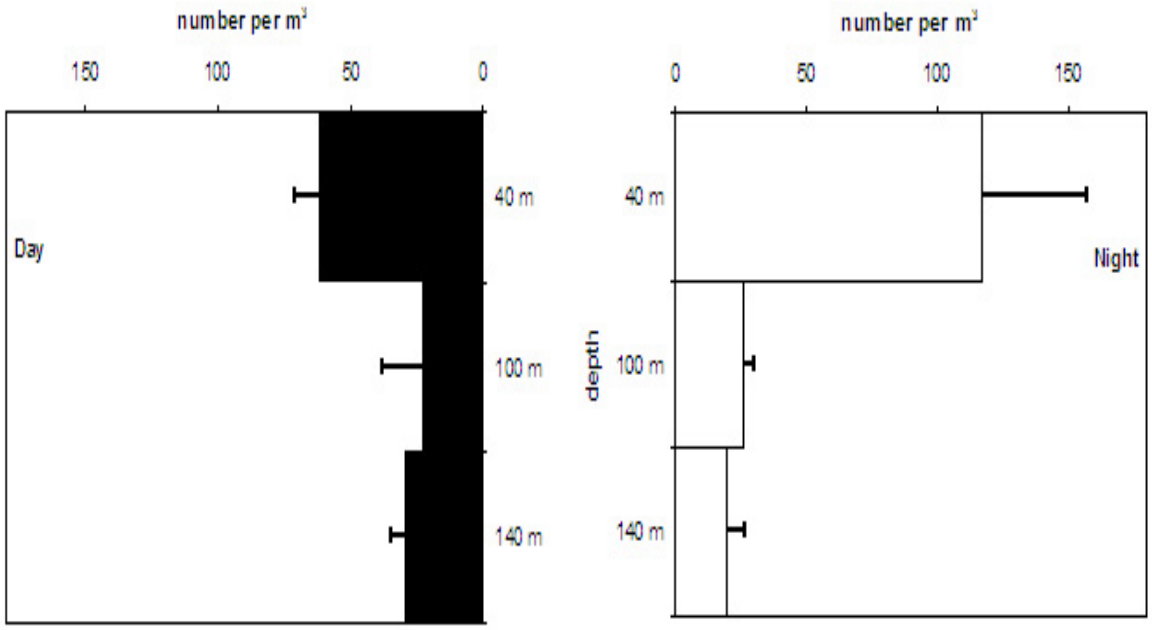

A) Shallow day
chaetognath
euphausiid
nauplii
ostracod
jelly
cladocera
1
17
3
0 - 40
3
14
1
7.5
40 - 100
2
7
1
1
100 - 140
depth (m)
0%
20%
40%
60%
80%
100%
B) Shallow night
26
0 - 40
6
18
8
3.5
40 - 100
22
1
100 - 140
0%
20%
40%
60%
80%
100%
percent non-copepod zooplankon

Figure 11


number per m³
150
100
50
0
Day
40 m
100 m
140 m
number per m³
0
50
100
150
depth
40 m
100 m
140 m
Night