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Diel distribution of copepods across a channel of an overwash mangrove island

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Abstract

The distribution of copepod species and their nauplii was studied in a narrow, blind channel on an overwash mangrove island offshore of Belize. Copepodids were sampled with a pump at five stations across the channel during a diel cycle. Diel changes of copepodid stages II – VI were marked by horizontal dispersal of *Dioithona oculata*, the dominant species, from swarms in the prop roots along the shore during the day to the edge of the prop root habitat at night. Migration of copepodids back to the prop roots appeared to be controlled endogenously because change from a night to a daytime age structure began before first light. Mean copepodid stage at subsurface depths in the channel and prop root edge decreased from 4.2 (with 6.0 = all adults) to 2.9 at predawn to 1.1 during day. The oceanic *Oithona nana* and *O. simplex*, and the coastal zone *O. fonsecae* were evenly distributed with depth and distance from shore during day and night, with avoidance of prop root shoreline during day. These species were much less abundant than *Dioithona oculata* in the prop roots, but of comparable or greater abundance in the channel. Coastal zone *Acartia spinata* exhibited evidence of swarming. Nauplii, sampled with a 25μm plankton net, were dominated by harpacticoid (50%) and cyclopoid (34%) nauplii, which generally were more abundant at 1m than at the surface and more abundant at night than the day. Lagrangian current measurements indicated velocities at ebb tide twice those of flood tide (1.9 vs. 0.8 cm s^{-1}) and a minimal residence time of 5 days, which could result in advection of *D. oculata* nauplii out of the Lair Channel before their recruitment into swarms as copepodid stage II. Previously reported maximum swimming speeds of swarming *D. oculata* copepodid stages (2.0 cm s^{-1}) and greater densities in prop roots and near the benthos may help copepodids avoid advection. The swarming behavior and diel horizontal migration (or dispersal) reported for *D. oculata* appears analogous to that of limnetic zooplankton, which may swarm among macrophytes along shorelines during the day to avoid visual predators and disperse or migrate away from the shoreline at night.

Introduction

The zooplankton community in the Lair Channel which is located on the overwash island of East Twin Cay, Belize, appears dominated by a swarming copepod species, *Dioithona oculata*. During the day, this species forms conspicuous swarms within shafts of light that penetrate through the red mangrove canopy into the underwater prop root habitat (Ambler et al., 1991). All copepodid stages, except the first, are found in swarms, which form at dawn. Swarming individuals disperse at dusk into the channel adjacent to the mangrove shore. Mean densities of *D. oculata* in the prop root habitat are highest during the day in swarms (10 800 – 34 500 animals l^{-1}), but are also significantly higher for non-swarming individuals during the day (150 animals l^{-1}) and even night (23 animals l^{-1}) than for *D. oculata* found in other habitats (Ambler

et al., 1991; Buskey et al., 1996). In contrast, mean densities of *D. oculata* from surface plankton tows adjacent to the mangrove canopy were always <3 animals l^{-1}; mean density at night (2.7 animals l^{-1}) was higher than that at dusk (0.16 animals l^{-1}) or midday (0.08 animals l^{-1}). Therefore densities ranged over six orders of magnitude from animals in midday swarms to those in the plankton during midday. Densities have not been determined in epibenthic habitats where dioithonans may be abundant or for other copepod species which are present in the channel adjacent to the mangrove canopy. The present study is unique because other studies of zooplankton distribution in mangrove channels are from estuarine mainland ecosystems (Grindley, 1984; Robertson & Blaber, 1992; McKinnon & Klumpp, 1998), and here densities of swarming and non-swarming copepod species are compared using one sampling technique rather than focusing exclusively on swarming species. Furthermore, the extraordinary abundance of the swarming copepods raises the question of how these densities are maintained in a tidal system connected to the coastal ocean. The purpose of this study was to: (1) characterize the distribution of copepods in a cross section of a mangrove channel over a diel cycle, (2) compare distributions of swarming and non-swarming species, (3) measure currents during flood and ebb tide to estimate residence time in the mangrove channel, and finally, (4) estimate how advection might affect recruitment of *D. oculata* into swarms.

Methods

Study site

The distribution of copepod species and their nauplii was studied in the Lair Channel, a narrow arm of the Main Channel which extends into the eastern island of Twin Cays (16° 50′ N, 88° 05′ W) (Figs 1 and 2). Twin Cays belongs to a group of mangrove islands in the lagoon behind the barrier reef of Belize in a subtropical climate dominated by northeast trade winds except for 'northers' which are northwesterly continental winds during November to February. Trade winds dominate the circulation seaward of the barrier reef, where the general circulation is southerly with currents of 0.18 – 0.35 m s^{-1} (Wust, 1964). Currents on the Barrier Reef are strongly influenced by mixed semidiurnal tides, which have a dominant diurnal component (U.S. Naval Oceanographic Office, 1965; Kjerfve et al., 1982). Temperature and salinity measurements monitored near the drop-off of the reef crest near Twin Cays during 1996 ranged from 23.6 to 31.3 °C and from 33.3 to 37.3 o/oo (Koltes et al., 1998).

Hydrography of Twin Cays

In July 6–13, 1995, 70 Lagrangian current measurements were made using drifters drogued in the upper 0.5 m in the waters adjacent to Twin Cays. Each drifter was composed of a 0.05 × 0.30 m Styrofoam cylindrical float and a 0.50 m × 0.50 m × 0.0015 m stainless steel window-shade drogue. The drifters were weighted so that the float was half submerged. The ratio of the wetted to dry surface was 33:1. Positions were determined with a Garmin GPS 50 (Global Positioning System), which has an uncertainty of ± 0.001′ of longitude or latitude corresponding to ± 18 m. The drifters were deployed from a 4.3 m Boston Whaler and tracked for 1 – 24 h with most deployments less than 12 h.

Copepodid horizontal distribution

Copepodid stages I – VI (stage VI is the adult) were collected from 1 to 3 depths at five stations which formed a transect across the Lair Channel (Fig. 2). The five stations include the prop root habitat on the south side (SR), the edge of the mangrove canopy on the south side (SB), the center of the open channel (CH), the edge of the mangrove canopy on the north side (NB), and the prop root habitat on the north side (NR). For each transect, nine samples were taken: surface samples at the two prop root stations (2); surface and ~1 m at the two canopy stations (4); and surface, ~1 m, and ~2 m depths in the open channel (3). Samples were collected using a Jabsco pump (Model 6360-001) with a 1.27 cm diameter plastic hose. For samples taken in the channel and at the canopy edge, a weighted line was attached to the hose intake to maintain the desired depth. For the prop root samples, a swimmer determined the hose intake position. The flow rate of the pump was 20.8 l min^{-1} and sample duration was usually 2 min.

Samples from the five stations (nine total samples) were collected during four times (local time): night (1:45 AM – 2:57 AM), predawn (4:13 AM – 4:51 AM), early morning (6:05 AM – 6:45 AM) on 30 June 1993, and midday (1:34 PM – 3:17 PM) on 25 June 1993. Dawn sampling was begun before first light and

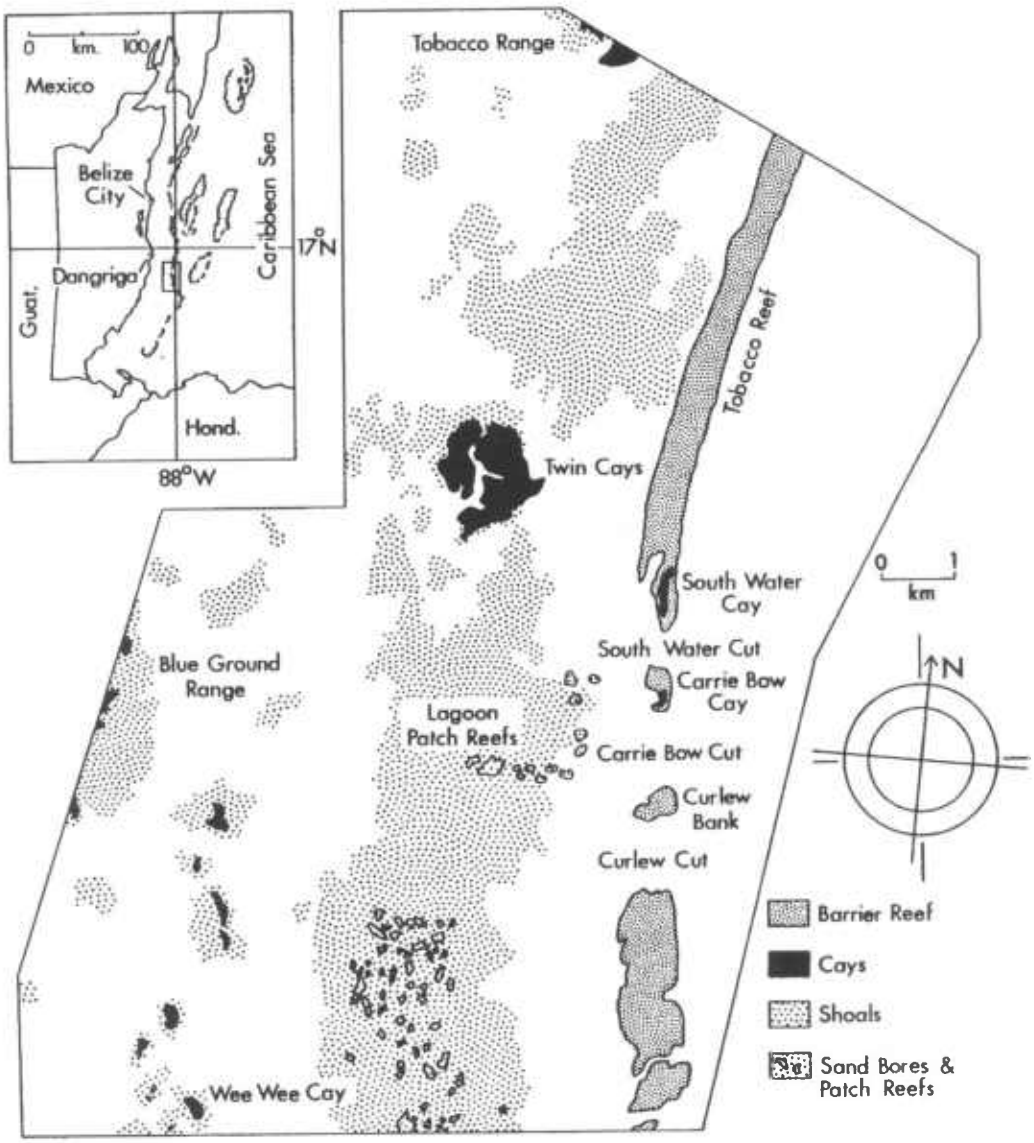

Figure 1. Study site at Twin Cays, a group of mangrove islands, located in the lagoon behind the Belize Barrier Reef. Study was based at the field station of the National Museum of Natural History, Smithsonian Institution at Carrie Bow Cay.

was completed before the sun was above the horizon. Sampling occurred during a high tide on 25 June 1993, and during a flood tide from 2:00 AM to 6:00 AM on 30 June 1993 (Fig. 3). Each depth at each station was sampled once during each time period, except the north and south roots stations during midday on 25 June when two swarms were sampled on each shore, and water adjacent to swarms on the south shore was sampled three times. Due to the high abundance of animals, sampling duration in swarms was shorter: swarms were sampled for 14–18 s; water adjacent to swarms was sampled for 30 s. Salinity and temperature were measured with a Solomat model 4007 module (platinum resistance temperature detector and conductivity sensor) at the nine depths during the night, early morning and midday sampling periods.

Animals from the pumped water were collected on a 45μm mesh screen, and preserved with 4% formaldehyde in ambient filtered water. In the laboratory, samples were transferred to a 4.5% propylene glycol 0.5% propylene phenoxitol solution for sorting, counting and final preservation. Ambient water

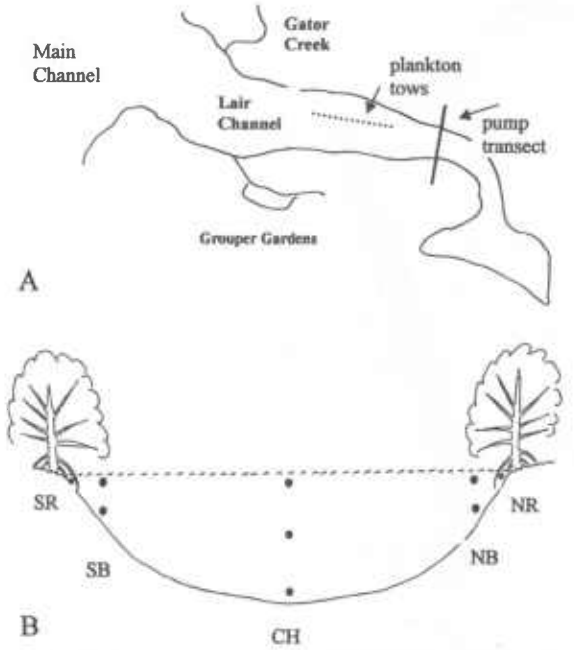

Figure 2. Lair Channel sampling locations in Twin Cays. (A) Cross section spanning the Lair Channel where copepodids were sampled with a pump (strained through a 45 μm mesh), and center channel where nauplii were sampled with a 25 μm plankton net. (B) Five zooplankton stations sampled at 1 –3 depths in cross section of Lair Channel, Eastern Twin Cay. View is looking towards the west. Stations labeled as SR=prop roots on south side, SB=under edge of mangrove canopy on the south side, CH=middle of Lair Channel, NB=under edge of canopy on the north side, NR=prop roots on north side.

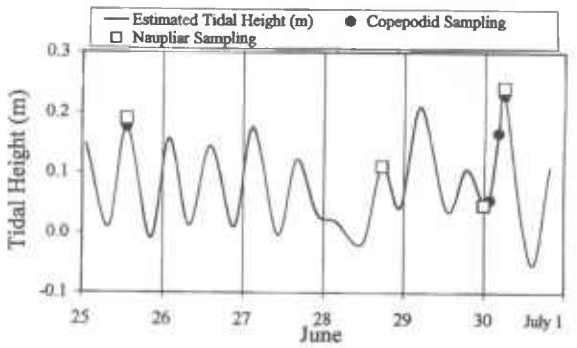

Figure 3. Estimated tidal heights for the Lair Channel with times for copepodid pump samples and naupliar plankton net samples noted. Tides were estimated from the nearest tide station at Punta Gorda, Belize. The distance between the shelf edge and Punta Gorda was similar to the distance between between Punta Gorda and Dangriga, so the time for the tide to propagate shoreward from the shelf edge was about the same time as the propagation of the tide north to the latitude of Twin Cays.

was replaced with de-ionized fresh water. Aliquots for counting were taken by suspending samples in a 100 ml graduated cylinder and drawing off 10 ml increments with a pipette until at least 100 copepodids were counted, or the whole sample was counted. Oithonid copepodids were staged, and gender of adults determined following Ferrari & Ambler (1992), and the acartiids following Sabatini (1990). Specimens were returned to a 4.5% propylene glycol 0.5% propylene phenoxitol solution for final preservation after counting. Mean copepodid stage was calculated as the sum of the number of copepodids of a particular stage multiplied by stage number (1 for copepodid I, 2 for copepodid II, etc.) divided by the total number of copepodids.

Naupliar sampling

Nauplii were collected from a central station in the Lair Channel (Fig. 2A). A series of 24 plankton samples using a 0.15 m diameter Nansen net with a 25μm mesh was taken at 1:00 AM, 5:00 AM, 1:00 PM and 5:00 PM hours local time. Three replicate tows at the surface and at 1 m were taken within a 10 min period. The midday samples were taken on June 25, the dusk samples on June 28 and the night and dawn samples on June 30, 1993. These times represented various tidal stages (Fig. 3).

The volume of water sampled was determined from elapsed sampling time and speed of plankton net speed as determined from the boat's bow wave using an L-shaped tube, one leg of which is perpendicular to the water surface and calibrated to measure the height of the bow wave. Elapsed sampling time was one minute for all tows except the 5:00 AM samples, which were 2 min. Care was taken to keep the plankton tows short enough to avoid clogging the net. All samples were preserved with 4% formaldehyde in ambient water, and later transferred to a 4.5% propylene glycol 0.5% propylene phenoxitol solution for sorting and counting. For those samples with fewer than 300 nauplii, all nauplii were counted. In samples with more than 300 nauplii, aliquots of at least 300 specimens were counted. Counts ranged from 50 to 1000 individuals for each sample.

Analysis

Analytical figures were constructed with EXCEL graphics, and statistical analyses were done with MINITAB.

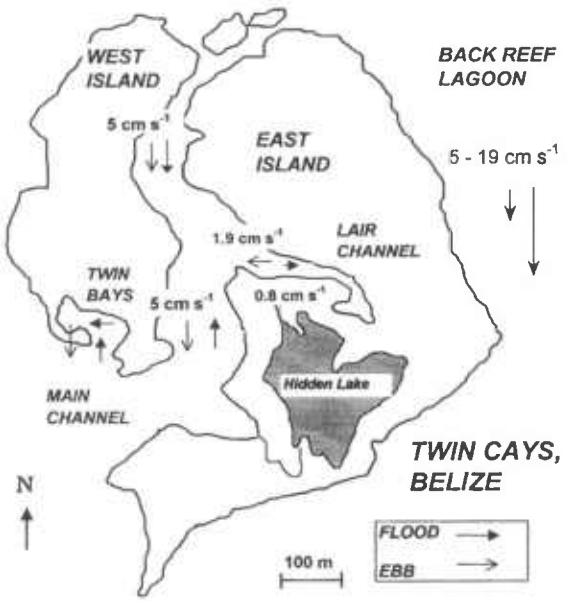

Figure 4. Circulation in Twin Cays on flood and ebb tides from Lagrangian drifters.

Results

Hydrography of Twin Cays

In the back reef lagoon, 16 surface current measurements indicated that the islands of Twin Cays are imbedded in a southward flowing current 5 – 19 cm s^{-1} (Fig. 4). Twelve surface current measurements in the Main Channel revealed that north of the entrance to the Lair Channel, flow was south at all times with a mean speed of 5 cm s^{-1} (3.0 – 5.7 cm s^{-1}). South of the entrance to the Lair Channel, flow was north on the flood tide at 5 cm s^{-1} (one observation) and south at 5 cm s^{-1}on the ebb tide (2.4 – 12.3 cm s^{-1}). In the Lair channel 28 surface current measurements indicated that the mean of eastward flowing flood tides was 0.8 cm s^{-1} (0.4 – 1.4 cm s^{-1}), while the mean for westward flowing ebb tides was 1.9 cm s^{-1} (0.6 – 5.4 cm s^{-1}).

Copepodid horizontal distribution

Zooplankton samples included five species: *Acartia spinata*, a calanoid; *Oithona fonsecae*, *O. simplex*, *O. nana*, and *Dioithona oculata*, oithonid cyclopoids. The most abundant species, *D. oculata*, was usually found in the prop roots and mangrove canopy edge; the other species usually were found at the edge of the mangrove canopy and the channel. Salinity and temperature were nearly constant with depth and varied only slightly between sampling dates (Table 1).

Table 1. Mean salinity and temperature of the nine samples collected during time periods of 1:45 AM June 30, 6:05 AM June 30, and 1:30 PM June 25. No data (nd) were collected at 4:13 AM June 30. Mean ± standard deviation for nine samples collected in cross section of Lair Channel (see Fig. 2)

Date	Time	Salinity (psu)	Temperature (°C)
30 June 93	1:45 AM	35.7 ± 0.3	27.6 ± 0.1
30 June 93	4:13 AM	nd	nd
30 June 93	6:05 AM	35.9 ± 0.2	27.5 ± 0.1
25 June 93	1:30 PM	35.6 ± 0.0	29.8 ± 0.4

Distribution of *A.spinata* in the Lair Channel was different between the day (6:05 AM and 1:30 PM) and night (1:45 AM and 4:13 AM) samples (Fig. 5, Table 2). At night, copepodids were rather evenly distributed, but they appeared to avoid the roots, except the north roots (NR). During the day, copepodids appeared to avoid the surface, except the north branches (NB) at midday. Highest densities, >5 copepodids l^{-1} were collected close to the substrate at bottom depths in the channel and mangrove branches stations (BR and CH), except at 1:45 AM when copepodids were evenly distributed in the channel. High densities were found close to the substrate, during the day and night.

Distribution of the three *Oithona* species was much more uniform than that of *Acartia spinata*. Densities of *Oithona* spp. were always the same order of magnitude, with a range of 1.4 to 3.7 l^{-1} (Fig. 5, Table 2). *Oithona* spp. were absent from prop root habitats during the day and sometimes at night. These species always inhabited the water column in the channel, day and night, and usually were found at the edge of the mangrove canopy.

Dioithona oculata dominated the mangrove root habitat of Lair Channel during the day (6:05 AM and 1:30 PM), when adults were found almost exclusively in swarms up to 1397 adults l^{-1} (Fig. 6, Table 3). At night, adults were still found at greatest densities in the roots, but densities were greater than during the day by over an order of magnitude at all depths. By 6:05 AM the daytime pattern had been established with most of the adults in swarms among the roots. The same distribution was observed for copepodid stages II–V, although their greatest densities were lower than those

Table 2. Number per liter of all copepodid stages (C1 – C6 adults) for *Acartia spinata*, *Oithona simplex*, *Oithona nana*, and *Oithona fonsecae* during four time periods: 1:45 AM, 4:13 AM, 6:05 AM, and 1:30 PM. Copepods were sampled with a pump at five locations across the Lair Channel: SR and NR (surface only), SB and NB (two depths), and CH (three depths). Nine samples were collected at each time period (see Fig. 2)

Acartia spinata, all stages, No l^{-1}						*Oithona simplex*, all stages, No l^{-1}					
1:45AM	SR	SB	CH	NB	NR	1:45AM	SR	SB	CH	NB	NR
0.0	0.0	0.1	1.3	0.5	0.1	0.0	0.0	1.7	2.0	1.4	2.1
1.3		0.2	1.4	1.0		1.3		0.0	1.4	1.9	
1.8			1.6			1.8			1.5		
4:13AM	SR	SB	CH	NB	NR	4:13AM	SR	SB	CH	NB	NR
0.0	0.0	0.1	0.5	0.2	2.1	0.0	0.0	2.1	1.9	1.4	0.0
1.3		0.0	0.7	1.6		1.3		0.0	2.2	2.3	
1.8			5.1			1.8			2.6		
6:05AM	SR	SB	CH	NB	NR	6:05AM	SR	SB	CH	NB	NR
0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	1.9	1.9	0.0	0.0
1.3		9.7	0.1	0.4		1.3		2.0	2.3	0.0	
2.4			1.8			2.4			2.2		
1:30PM	SR	SB	CH	NB	NR	1:30PM	SR	SB	CH	NB	NR
0.0	0.0	0.0	0.1	0.1	0.0	0.0	3.5	2.2	2.1	0.0	0.0
1.3		0.4	0.6	5.1		1.3		3.5	3.3	1.9	
2.4			8.5			2.4			3.2		
Oithona nana, all stages, No l^{-1}						*Oithona fonsecae*, all stages, No l^{-1}					
1:45AM	SR	SB	CH	NB	NR	1:45AM	SR	SB	CH	NB	NR
0.0	0.0	2.2	2.6	1.7	2.0	0.0	3.3	2.3	2.9	2.6	2.2
1.3		1.5	2.4	1.6		1.3		2.5	2.7	2.4	
1.8			2.1			1.8			2.3		
4:13AM	SR	SB	CH	NB	NR	4:13AM	SR	SB	CH	NB	NR
0.0	0.0	2.1	2.5	1.9	2.7	0.0	0.0	0.0	2.5	2.3	2.4
1.3		0.0	2.5	2.9		1.3		0.0	2.6	1.4	
1.8			3.1			1.8			1.6		
6:05AM	SR	SB	CH	NB	NR	6:05AM	SR	SB	CH	NB	NR
0.0	0.0	2.1	2.2	2.3	0.0	0.0	0.0	1.4	2.2	1.4	0.0
1.3		2.9	2.5	2.2		1.3		0.0	2.3	1.7	
2.4			2.6			2.4			1.9		
1:30PM	SR	SB	CH	NB	NR	1:30PM	SR	SB	CH	NB	NR
0.0	0.0	2.9	2.9	2.7	0.0	0.0	0.0	2.9	1.4	2.0	0.0
1.3		3.5	3.7	3.1		1.3		3.0	2.9	3.2	
2.4			3.1			2.4			3.1		

of adults, e.g. 420 copepodid stage V l^{-1} and 283 copepodid stage III l^{-1} (Fig. 6, Table 3).

Copepodid stage I of *D. oculata* (Fig. 6, Table 3) exhibited a distribution which differed from older copepodids. During the day these copepodids generally were found near the benthos and were not as abundant in the swarms as were the older copepodid stages. At 6:05 AM, a maximum of 11.5 l^{-1} was found

Table 3. Number per liter of *Dioithona copepodid* adults (CVI), copepodid five (CV), copepodid three (CIII), and copepodid one (CI) during four time periods: 1:45 AM, 4:13 AM, 6:05 AM, and 1:30 PM. Copepods were sampled with a pump at five locations across the Lair Channel: SR and NR (surface only), SB and NB (two depths), and CH (three depths). Nine samples were collected at each time period (see Fig. 2). Densities for SR and NR samples are mean densities ($n = 2$) from swarms collected at 1:30 PM. and density in parentheses below SR for 1:30 PM is mean density ($n = 3$) for samples collected in water adjacent to swarms

Dioithona oculata adults						*Dioithona oculata*, CV					
1:45AM	SR	SB	CH	NB	NR	1:45AM	SR	SB	CH	NB	NR
0.0	55.5	0.7	0.7	0.6	4.0	0.0	4.3	0.3	0.2	0.2	0.2
1.3		0.7	1.2	1.8		1.3		1.1	0.2	0.8	
1.8			1.2			1.8			0.3		
4:13AM	SR	SB	CH	NB	NR	4:13AM	SR	SB	CH	NB	NR
0.0	125.0	17.6	0.3	1.2	10.5	0.0	13.2	2.3	0.1	0.3	2.3
1.3		41.1	0.2	0.4		1.3		5.1	0.1	0.1	
1.8			0.2			1.8			0.1		
6:05AM	SR	SB	CH	NB	NR	6:05AM	SR	SB	CH	NB	NR
0.0	1397.8	0.7	0.1	0.0	80.9	0.0	185.1	0.1	0.0	0.0	20.0
1.3		0.1	0.0	0.0		1.3		0.0	0.0	0.0	
2.4			0.0			2.4			0.0		
1:30PM	SR	SB	CH	NB	NR	1:30PM	SR	SB	CH	NB	NR
0.0	762.3	0.1	0.0	1.6	961.3	0.0	270.3	0.0	0.0	0.5	420.6
1.3	(59.5)	0.1	0.0	0.0		1.3	(15.04)	0.0	0.0	0.0	
2.4			0.1			2.4			0.0		
Dioithona oculata, CIII						*Dioithona oculata*, CI					
1:45AM	SR	SB	CH	NB	NR	1:45AM	SR	SB	CH	NB	NR
0.0	0.2	0.2	0.8	0.3	0.1	0.0	0.0	0.0	0.6	0.1	0.0
1.3		0.2	0.4	1.2		1.3		0.1	0.3	0.4	
1.8			1.1			1.8			0.4		
4:13AM	SR	SB	CH	NB	NR	4:13AM	SR	SB	CH	NB	NR
0.0	5.4	1.1	0.3	0.3	6.7	0.0	0.0	0.1	0.2	0.2	1.4
1.3		7.2	0.4	0.7		1.3		0.7	0.9	2.1	
1.8			0.1			1.8			1.1		
6:05AM	SR	SB	CH	NB	NR	6:05AM	SR	SB	CH	NB	NR
0.0	81.7	0.1	0.1	0.0	44.9	0.0	0.0	0.0	0.1	0.1	1.6
1.3		0.0	0.0	0.0		1.3		11.5	0.4	0.7	
2.4			0.0			2.4			1.7		
1:30PM	SR	SB	CH	NB	NR	1:30PM	SR	SB	CH	NB	NR
0.0	283.7	0.1	0.0	1.5	242.6	0.0	3.5	0.4	0.0	0.2	0.0
1.3	(27.6)	0.0	0.0	0.0		1.3	(0.62)	5.2	2.8	0.7	
2.4			0.2			2.4			0.9		

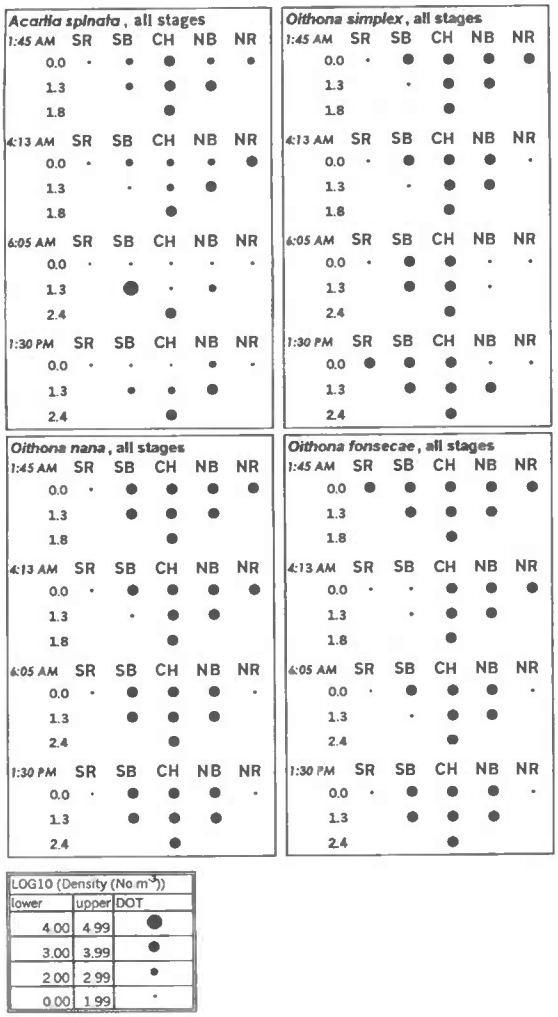

Figure 5. Distribution (Log $_{10}$ density (No. m^{-3})) of copepodid and adult stages of *Acartia spinata*, *Oithona simplex*, *Oithona nana*, and *Oithona fonsecae* at four time periods and five locations, spanning a cross section of the Lair Channel (see Fig. 2). Size of dots represents the order of magnitude. Zero values shown for Log $_{10}$ density values <2.0, since these values represent <10 animals counted in a sample.

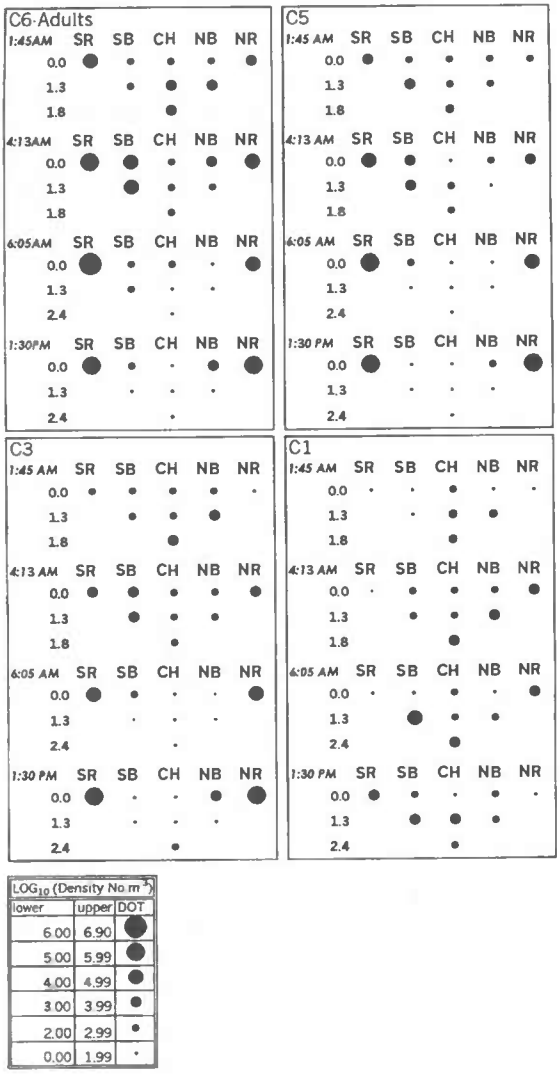

Figure 6. Distribution (Log $_{10}$ density (No. m^{-3})) of *Dioithona oculata* adults (CVI), copepodid stages five (CV), three (CIII), and one (CI) at four time periods and five locations, spanning a cross section of Lair Channel (see Fig. 2). Size of dots represents the order of magnitude. Zero values shown for Log $_{10}$ density values < 2.00, since these values were always <10 animals counted in a sample.

under the south branches (SB) close to the benthos. At night, greater densities were observed in the channel (CH) and under the north branches (NB) close to the benthos.

Mean copepodid stage for *D. oculata* is shown (Fig. 7) for the four different sampling times at four averaged localities: north and south roots, surface and 1m under north and south branches, three depths in the channel, and four subsurface depths under the branches and in the channel. Mean copepodid stage was the highest in the prop roots. Comparisons of mean stage values in the root habitat for (1) day (n = 6) *versus* night (n = 4) time periods, and (2) swarming animals (n = 6) *versus* non-swarming animals (n = 3) were not significantly different (t tests, $P < 0.05$). In the branches and channel sites, mean copepodid stage values at night (1:45 AM and 4:13 AM) were the same and both were higher than early morning and midday, which were the same (one-way ANOVA each for branch and channel locations). The diel pattern for subsurface areas which included branches and channel

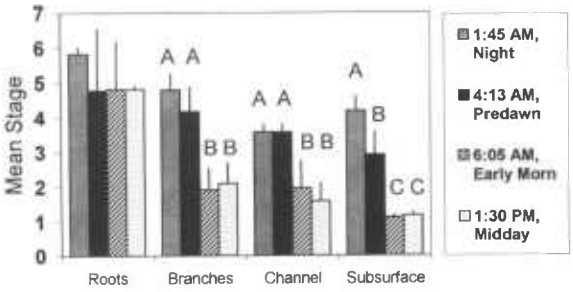

Figure 7. Mean stage ± S.E.for *Dioithona oculata* at four time periods and four locations. Roots = prop root samples (SR and NR, $n = 2$, range instead of S.E. except for 3:30 PM, $n = 4$). Branches = edge of mangrove canopy (SB and NB, $n = 4$). Channel = center channel (CH, $n = 3$). Subsurface = depths below the surface of SB, NB, and CH, $n = 4$). See Figure 2. Capital letters above bars denote results of Fisher's pairwise comparisons ($P < 0.05$) for one-way ANOVA for Branches, Channel and Subsurface locations.

sites, was different than the other locations: highest mean copepodid stage was at night (4.18), predawn (2.91) was slightly but significantly lower, and lowest values were at early morning (1.10) and midday (1.16).

Copepod nauplii

A total of 45 854 copepod nauplii from 24 samples in the Lair Channel were identified to copepod order and enumerated (Fig. 8). Several factors affected naupliar densities: time of day, depth, copepod order, and interaction of time of day on depth (Table 4). Harpacticoid nauplii were the most numerous in all samples, comprising 49.5% of all nauplii; cyclopoids comprised 34.3%; and calanoids were least abundant, 16.3% of the total. The proportion of each order did not vary between time of day and depth, except for the calanoid nauplii which consistently comprised a greater proportion at the surface than at 1 m (Fig. 8B, Table 4A – interaction of copepod order and depth). Overall, densities were greater at 1m than the surface, and densities were greater at night than day (Fig. 8A, Table 4A). Densities of copepod nauplii fluctuated in a diel cycle consistent with a short vertical migration at dusk (5:00 PM) when naupliar densities were greater at the surface than 1m. At other times, this distribution was reversed with naupliar densities greater at 1m than the surface. These differences with depth were statistically significant except for midday (1:00 PM) when high variability between replicates resulted in no difference between densities at the two depths (Table 4B). Patterns of temporal variation in the vertical distribution within calanoid, cyclopoid and harpacticoid

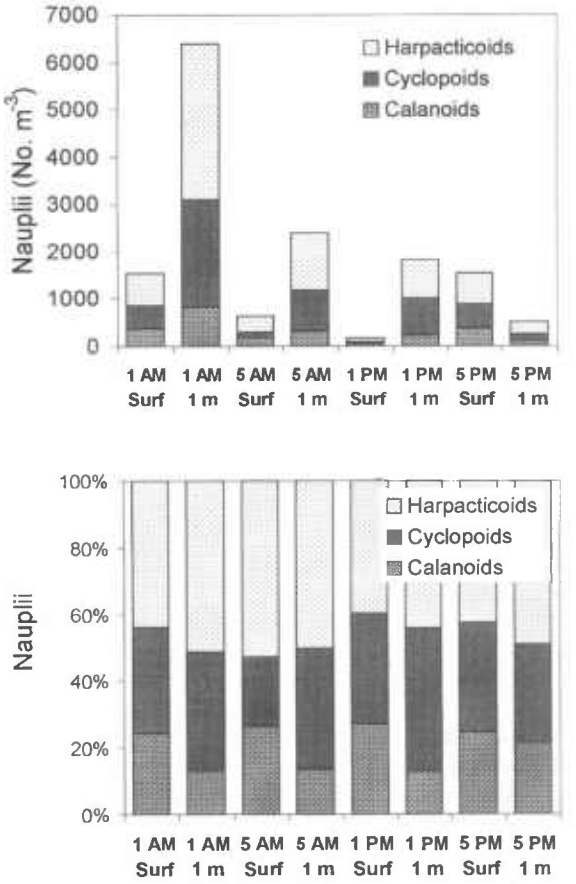

Figure 8. Mean density ± S.E.of nauplii (No. m^{-3}), top, and relative abundance, bottom, for nauplii collected in the center of the Lair Channel during four time periods (Fig. 2). See text and Table 4 for statistical analysis.

nauplii were the same for each of the orders as for the totals (Table 4A – no significant interaction between copepod order and time of day).

Discussion

Copepod species found in the Lair Channel have different oceanographic affinities. *Oithona nana* is a morphologically gracile oithonid cyclopoid with a urosome almost as long as the prosome (Nishida, 1985), while *O. simplex* is a stocker, deeper-bodied oithonid with a urosome much shorter than the prosome; both are epipelagic, oceanic oithonid cyclopoids with circumglobal distributions. *Oithona fonsecae* is a coastal zone oithonid usually found in estuaries and lagoons (Ferrari & Bowman, 1980). Despite these differences, distributions of the three oithonids in the Lair Chan-

Table 4. Analysis of variance (ANOVA) for naupliar densities in the Lair Channel

(A) Three-way ANOVA (copepod order, time of day, and depth) with interactions for density of nauplii in the Lair Channel. $^*P < 0.05$

Factor	F value	P value	Comment
Copepod order	9.02	<0.05	*Harpacticoids most abundant
Time of day	16.68	<0.05	*Nauplii most abundant at night
Depth	27.30	<0.05	*Nauplii more abundant at 1 m
Interaction copepod order and time of day	1.81	0.12	Orders show same diel pattern
Interaction copepod order and depth	4.42	0.02	*Orders different depth patterns
Interaction time of day and depth	12.04	<0.05	*Diel migration
Three way interaction	1.46	1.46	Not significant

(B) Further analysis for diel migration which was a significant interaction of time of day and depth in Table 4A. F values for two-way ANOVA (copepod order, depth, and interaction of order and depth): one for each time of day to test differences in depth distribution for the three copepod orders. $^*P < 0.05$

Time of day	Copepod order	Depth	Order × Depth
1:00 AM	0.011*	<0.05*	0.041
5:00 AM	0.003*	<0.05*	0.022*
1:00 PM	0.724	0.125	0.751
5:00 PM	0.009*	<0.05*	0.497

nel were quite similar (Fig. 5, Table 2). *Dioithona oculata* is a tropical oithonid with a circumglobal distribution in coastal zone areas (Nishida, 1985); it is the most abundant species in the Lair Channel, forming extensive swarms under the mangrove prop roots. *Acartia spinata* is a coastal zone acartiid calanoid often collected in large swarms in the vicinity of coral reefs (Hamner & Carleton, 1979); it is not as abundant as *D. oculata*. Swarming copepod species have been found in many tropical habitats (Ambler, 2002), but most such species from these areas have not been well studied.

Although salinity of the Lair Channel was similar to oceanic areas and Twin Cays is adjacent to the Belize Barrier Reef, species richness in the Lair Channel was much lower than that found in tropical oceanic waters (McGowan & Walker, 1979; McKinnon, 1991). Copepod species composition in the Lair Channel was most similar to the marine species group described for tidal creeks flowing through coastal mangrove forests (Grindley, 1984; Robertson & Blaber, 1992; McKinnon & Klumpp, 1998) except that swarms were not described for tidal creeks.

No attempt was made to identify species of nauplii. However, polyarthran harpacticoids, longipediids or canuellids, made up a significant proportion of harpacticoid nauplii in these and similar planktonic habitats (Fornshell, 1994). Because copepodids of *A. spinata* were the only calanoids encountered in the Lair Channel, calanoid nauplii probably belonged to this species. Copepodids of *D. oculata* dominated the cyclopoid species, and thus probably were the dominant naupliar species of cyclopoid.

Densities of *D. oculata* reported in the present study sometimes differed appreciably from those of Ambler et al. (1991) who sampled similar prop root habitats; these density differences probably reflect differences in sampling gear. The mean density of *D. oculata* within swarms sampled with the pump in the present study, 1617 animals l^{-1} ($n = 6$), was appreciably less than the mean density from samples taken with plastic bags in Ambler et al. (1991), 10 800 animals l^{-1} ($n = 6$). Although we did not observe dioithonans avoiding the pump intake, the pump was apparently sampling water outside of the swarm, as well as in the swarm itself. To a lesser degree, a dilution effect also was noted by Buskey et al. (1996) when densities calculated by image analysis (34 500 l^{-1}) were compared to densities taken with plastic bags (10 800 l^{-1}). Further support for a dilution effect for dioithonans sampled with a pump can be found by comparing samples of non-swarming dioithonans in open water at night and in water adjacent to swarms during the day, habitats from which the location of the pump intake was assumed not to bias the sampling of dispersed animals. From the three depths in the

channel at night, there was no appreciable difference between density from pump samples, 3.2 l^{-1} ($n = 6$) *versus* a plankton net, 2.7 l^{-1} ($n = 3$, Ambler et al., 1991). Densities were similar for water sampled adjacent to swarms during the day: 137 l^{-1} ($n = 3$) with the pump and 150 l^{-1} ($n = 6$) with plastic bags (Ambler et al., 1991). However, mean density from plankton nets towed near the surface in the channel during the day, 0.08 l^{-1}, ($n = 3$, Ambler et al., 1991), was lower than mean density from pump samples in the three channel depths during the day, 1.1 l^{-1} ($n = 6$) but similar to pump samples at the surface, 0.1 l^{-1} ($n = 2$). Dioithonans avoided surface waters during the day but not at night, so that Ambler et al. (1991) underestimated mean density in the channel by sampling only at the surface.

Buskey et al. (1995) effected swarm formation in the laboratory during the day with dioithonan copepodids, but could not elicit a similar response with the same stimuli at night. They inferred from these experiments that swarm formation of *D. oculata* is endogenously controlled. In the present study and Ambler et al. (1991), *D. oculata* dispersed from the root area at night and reformed swarms at dawn. This recovery behavior of the copepods to the root area is not easily amenable to experimental manipulation. Therefore, evidence of endogenous control of this recovery was sought from changes in the age structure at predawn (4:13 AM) relative to that at night (1:45 AM), and which might anticipate the age structure during the day (6:05 AM and 1:30 PM). Evidence for the endogenous control of this recovery can be seen in the change in mean stage in the subsurface depths (Fig. 7) from a night mean stage of 4.18 to a mean stage of 2.91 before first light (4:13 AM), and then day values of mean stage, 1.10 and 1.16. These differences between night, predawn and day samples were statistically significant, in contrast to the branches and channel categories which only had significant differences between day and night samples (Fig. 7). Thus, dioithonans had begun to effect a change in their age structure from night toward their age structure during the day before they received a direct stimulus from sunlight.

Tidal currents were dominant in the confined waters of the Lair Channel, with a 2:1 ratio of outflow to inflow velocities. Residence time can be approximated because the volume of the Lair Channel (~35 200 m^{-3}) and the measured mean inflow velocity (0.8 cm s^{-1}) are known. Residence time is 5.1 days for a model with no mixing and complete replacement, or 5.1 days to replace 63% of the Lair Channel volume for a model with instantaneous mixing (Knauss, 1978). In reality, residence time is expected to be even longer because mixing cannot be instantaneous in a long narrow channel like Lair Channel. A residence time greater than five days is in the time of scale of copepod development and has implications for retention of a population of *D. oculata* in Lair Channel.

Nauplii of *D. oculata* were not collected with copepodids in swarms or in the root areas (Ambler et al., 1991), but were found in the channel waters (Fig. 8). Ambler et al. (1999) reported that nauplii hatched from their egg sacs at night when females were more likely to be dispersed into water adjacent to the prop roots (Fig. 6, Table 3), and that nauplii can be eaten by older copepodids, including adult females, which is more likely in a swarm. Development of *D. oculata* from nauplius 1 to nauplius 5 takes 3.8 days at 31 °C (Ferrari & Ambler, 1992). Assuming isochronal growth for oithonids (Sabatini & Kiørboe, 1994), and extrapolating from development time reported for nauplii of *D. oculata* from Ferrari & Ambler (1992), the development time from egg hatching to the first swarming stage (copepodid II), is 7.9 days at 31 °C. Thus a circulation model in which Lair Channel water was replaced completely during a period of tidal exchange with non-instantaneous mixing would allow most of the non-swarming stages to develop in the Lair Channel and be recruited into swarms before being advected to the Main Channel. In addition, non-swarming stages would be less likely to be advected out of the Lair Channel because nauplii of cyclopoid copepods and dioithonan copepodid stage 1 were much more abundant at 1 m, where water movements close to the bottom are assumed to be slower, than the surface (Figs 6 and 8, Table 3).

Swarming copepodids might be advected out of the Lair Channel and into the Main Channel where they would be lost from Twin Cays on ebb tides, when currents are twice as great as flood tides, and at night when they disperse away from the root areas. However, the potential advection of swarming animals out of the Lair Channel is ameliorated in the following ways. Densities at night remain as high or higher in the root area than in adjacent surface waters under the branches or in the channel (Fig. 6, Table 3), suggesting that many copepodids do not disperse from the root area and into the channel at night, and thus would not be subject to this model of advection. Other copepodids that dispersed from the root area at night, e.g. females with embryos in egg sacs, may remain

closely associated with the benthos (Fig. 6, Table 3), where tidal velocities are assumed to be lower. Furthermore, in laboratory experiments, Buskey et al. (1996) found that copepodids from field-collected swarms are able to swim up to 2 cm s^{-1}, which is comparable to the mean ebb tide current velocity measured in the Lair Channel. Such animals being advected toward the Main Channel might be able to reduce the effects of advection on the ebb tide by swimming until a flood tide could return them to an area propitious for swarming.

The main purpose of this study was to compare distribution and abundance of naupliar and copepodid stages of copepod species in the Lair Channel. A limitation of our study was that we did not sample over diel cycles during both high and low tides (Fig. 3). Tidal stage probably did not strongly affect the results because samples were collected along a cross section of the Lair Channel, perpendicular to tidal currents, and near the Lair, the blind end of the channel. Significant differences were found in abundance and mean stage between day and night, and between different depths for *D. oculata* (Fig. 7). Although mean stage values for the prop root samples were the same for day and night, pump samples underestimated swarm densities. The volume of prop root habitat occupied by swarms was not determined in the present study; it might influence the abundance of copepodids in Table 3 but not the value of mean stage which was the same for swarming and non-swarming animals in the prop roots.

These data suggest that some *D. oculata* disperse from the root areas at night and reassemble back to the root areas during the day (Fig. 6, Table 3), and that the three *Oithona* spp. avoid the root areas during the day, but may occupy these areas at night (Fig. 5, Table 2) at very low densities relative to *D. oculata*. Because planktivorous fish are found in water at the edge of the mangrove canopy (Ambler et al., 1991), swarming by dioithonans may be a predator defense strategy. Young barracuda which are territorial, patrol the mangrove edge and often attack planktivorous fish, so the latter must remain in their schools rather than feed on dioithonans. Diel horizontal migration (DHM), similar to that of the dioithonans, has been reported for cladocerans in many lakes, either as 'shoreline avoidance' during the day and migration to shallow water in the littoral zone at night, or as aggregations in the littoral zone during the day and migration to deeper water at night (Jeppesen et al., 1998). There is no concensus about the cues causing this pattern but this DHM may result from a response to: density of macrophytes in the littoral zone which can be a refuge for zooplankton from visual fish predators; density of planktivorous fish which causes cladocerans to seek refuge in the macrophytes, presence of piscivorous fish which causes planktivorous fish to seek refuge in the macrophytes and so force cladocerans to leave; and the size of the cladocerans because planktivores prefer larger sized species. These factors may shape behavior of the copepod species in the mangrove channels studied here because *D. oculata* and *A. spinata*, the larger copepods, form swarms in the nearshore prop root areas, while the smaller copepods, three *Oithona* spp., are rarely found in the prop root habitat during the day.

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