Population structure and swarm formation of the cyclopoid copepod *Dioithona oculata* near mangrove cays

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Abstract. The cyclopoid copepod *Dioithona oculata* forms swarms in water <30 cm deep among prop roots of red mangroves (*Rhizophora mangle*) which fringe protected areas of two lagoonal cays, Twin Cays, Belize. During 7 of 8 months surveyed by *in situ* observation, swarms were present but differed in size from small cylindrical swarms (5–10 cm diameter) to bands extending up to 1200 m. Swarms were never observed at night. Swarms formed at dawn when light intensities reached an average value of 13.82 ($\log_{10}$ quanta cm^{-2} s^{-1}) and dispersed at dusk at similar intensities. Swarms observed in June formed earlier and dispersed later in the day than swarms observed in January; their swarming behavior followed seasonal changes in light intensity. Mean dioithonan density in swarms (10 ml^{-1}) was much higher than the mean density (0.15 ml^{-1}) of non-swarming dioithonans around mangrove prop roots. In open water 3–5 m away from the mangroves, mean dioithonan density was 7.9×10^{-5} ml^{-1} during the day, and 2.68×10^{-3} ml^{-1} at night. Swarms were composed predominantly of adults and copepodid stages IV and V, although younger copepodid stages could be present. Nauplii were never present. The 'average copepodid stage' for all 95 swarms sampled was 5.3, where 6.0 represents a swarm with only adults. In open water 3–5 m away from the mangroves, the youngest copepodids (stage one) dominated the dioithonan population during the day. At night when swarms dispersed to open waters, average copepodid stage was higher (3.5) compared with the day value (1.2) in open waters. Although densities in swarms were higher in June than January, average copepodid stage in June was higher (5.6) than that in January (4.9). A higher percentage of adults were females during June than January. Therefore higher densities did not result from increases of smaller stages in swarms, but perhaps changes in behavior or population structure.

Introduction

Copepods have aggregated distributions on all space and time scales (Haury *et al.*, 1978). The most dense copepod aggregations are called 'swarms', a term usually applied to monospecific aggregations in which individuals are not oriented parallel to one another (Mauchline, 1971). Dense monospecific aggregations of individuals oriented parallel to one another are 'schools'. Numerous species of calanoid genera *Acartia*, *Centropages*, *Tortanus* and *Ridgewayia* form swarms (see Emery, 1968; Yeatman, 1969; Humes and Smith, 1974; Hamner and Carleton, 1979; Ueda *et al.*, 1983; Tanaka *et al.*, 1987a; Kimoto *et al.*, 1988). Three cyclopoid copepod species also aggregate in swarms, *Oithona nana*, *Oithona davisae* and *Dioithona oculata* (Emery, 1968; Hamner and Carleton, 1979; Omori and Hamner, 1982; Ueda *et al.*, 1983; Kimoto *et al.*, 1988; Hirota, 1990). *Labidocera pavo* is the only copepod species reported to form 'schools' (Omori and Hamner, 1982).

Copepod densities in swarms ranging from 0.10 to 3.32 copepods ml^{-1} have been reported for fine (1 cm–1 m) and micro (10–100 m) space scales (Emery, 1968; Hamner and Carleton, 1979; Ueda *et al.*, 1983). These swarms are composed predominantly of adults and copepodids but not nauplii (Hamner and Carleton, 1979; Ueda *et al.*, 1983). The swarms occurred near sea grasses, algal beds and coral reefs, in tropical and temperate areas, and could therefore be considered epibenthic. Copepod swarms have been observed only during the day. Dispersal at dusk was observed *in situ* for two temperate *Acartia* species (Ueda *et al.*, 1983). Dispersal has been inferred for swarming copepods near coral reefs by observing higher densities throughout the water column at night than during the day.

In this paper we describe swarms of *D.oculata* near prop roots of red mangrove, *Rhizophora mangle*, on lagoonal cays of Belize. Copepodid stage distribution of swarming dioithonans is compared with that of non-swarming animals also found near prop roots, and to that of non-swarming animals found in open water 3–5 m away from the mangroves. Evidence is presented for the formation of swarms during the day and dispersal of swarms at dusk. Light intensity is quantified during these periods to consider its effect on swarm formation and dispersal, and packing of individuals in a swarm. Seasonal differences in copepodid stage structure and density in swarms were found for samples collected at the same site.

Method

Research site

Swarms of *D.oculata* were studied around two mangrove islands, Twin Cays (~16°50'N, 88°05'W), found within the 25 km wide lagoon behind the barrier reef off Belize, Central America (Figure 1). Twin Cays are ~4 km from the Smithsonian Field Station at Carrie Bow Cay where this project was based (Reutzler and Feller, 1988). From April to November, weather on these cays is controlled by north-east trade winds. During December–March winds can shift to the north-west and weather is often influenced by continental air masses on the mainland. Most of the swarm observations reported here were made along the north shore of the outer (most eastern) bay of Twin Bays (Figure 2). This site is sheltered from the effects of trade winds and winds from land. Water temperatures surrounding the islands vary from 25°C in February to 32°C in June.

Field collection

Direct observations of *D.oculata* were made throughout waters surrounding Twin Cays on nine 1 week trips taken in May 1985, October 1985, March 1986, November 1986, February 1987, July 1987, January 1988, June 1988 and May 1989. Swarms were observed *in situ* by snorkeling among prop roots and overhanging branches of the red mangroves. Extensive visual searches for swarms were made in open waters and above turtle grass beds adjacent to the mangroves.
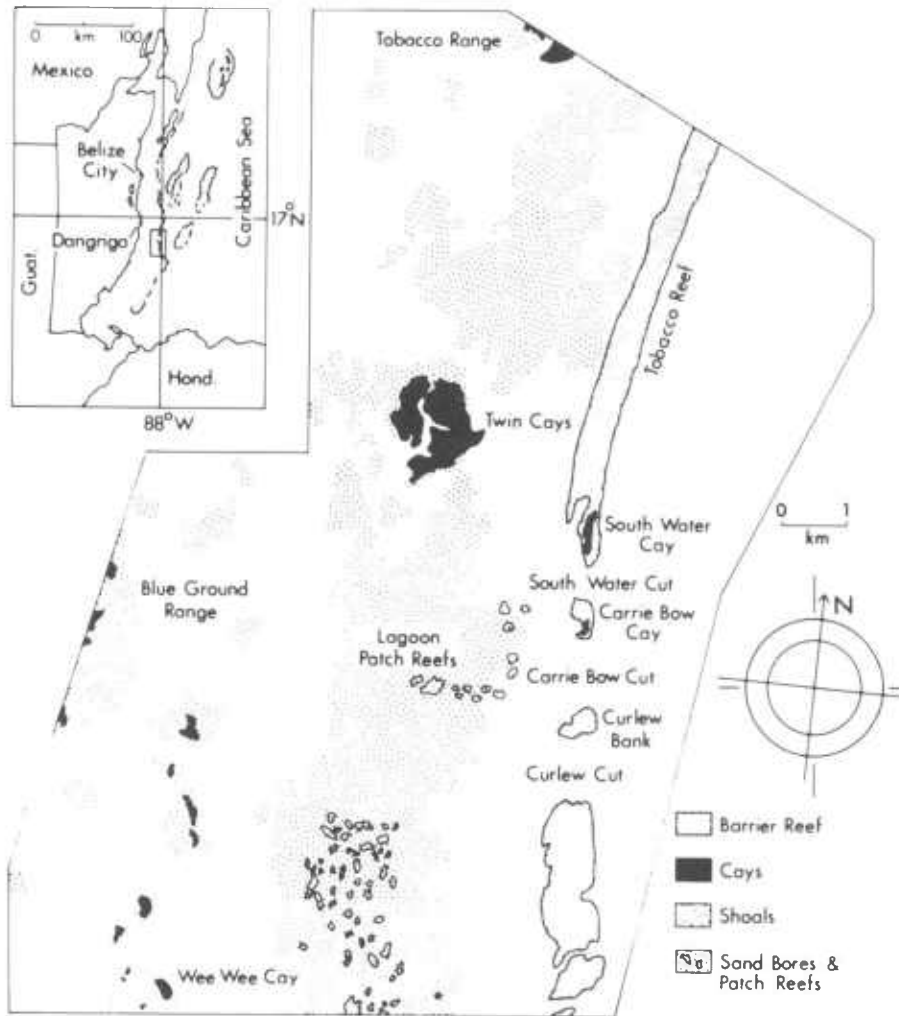
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Fig. 1. Location map of the mangrove cays (Tobacco Range, Twin Cays, Blue Ground Range and Wee Wee Cay) near the Smithsonian Institution's Field Station at Carrie Bow Cay. Square in inset indicates location along the coast of Belize. From Reutzler and Feller (1988).

Dioithonan swarms were visually identified near the mangrove prop roots and samples of 300–1100 ml were collected with plastic bags. Plastic bags were easy to use around the roots, because they could be submerged easily while collapsed, positioned close to a swarm, opened only enough to surround the swarm, and then either lifted to the surface or sealed underwater. During periods of very low light intensity, the swarm volume was more difficult to determine visually, and water adjacent to the swarm may have been collected thus underestimating swarm densities. In areas near the mangrove roots where no swarms were visually observed, 2–6 l of water were collected to obtain sample volumes of

Fig. 2. Twin Cays showing the presence (filled circle) or absence (open circle) of dioithonan swarms in the red mangrove prop root habitat. Filled triangle is the location of the dock. Scale: 2.3 cm on figure = 250 m.

non-swarming animals. Animals in the plastic bags were sieved from the water with a 110 μm screen for later enumeration. For many samples, the water collected with the swarms was saved to determine if nauplii were present, but they never were. Copepod density was calculated as number of *D.oculata* divided by the volume of water collected.

Samples of dioithonans were also collected with a hand-held net (18 cm diameter, 20 cm long, 110 μm mesh), which was swept through a swarm or water with non-swarming copepods over a known distance. Density was calculated as number of animals, divided by the water volume sampled which was the distance of the sweep times the mouth area of the hand-held net. On six occasions, paired samples were taken with the sealed plastic bags and hand-held nets to compare the sampling efficiency of the two methods.

Samples of *D.oculata* were also collected from open water ~3–5 m from the mangroves with a 0.5 m, 80 μm plankton net with a flow meter. A 35 m transect parallel to the shore in depths <1.5 m was traversed in 60–90 s. The net mouth was maintained in the upper meter and 6–8 m³ of water was filtered. Naupliar

Table I. Comparison of *D.oculata* collected in swarms taken with hand-held net (HN) and with plastic bags with seals (ZP)

Time	Sample type	Density (cop. ml^{-1})	Percent adult	Average copepodid stage
June 3, 1988, Outer Twin Bay, pre-swarms				
03.35	HN	0.016	93.2	5.80
03.32	ZP	0.021	91.9	5.73
03.40	HN	0.028	86.0	5.54
03.45	ZP	0.027	94.0	5.78
June, 4, 1988, Outer Twin Bay, swarms				
14.30	HN	1.01	90.6	5.80
14.30	ZP	5.12	90.0	5.78
July 4, 1987, The Lair, swarms				
14.30	HN	0.72	87.7	5.86
14.30	ZP	8.09	74.7	5.68
Nov. 19, 1986, Outer Twin Bay, swarms				
14.00	HN	1.22	26.6	4.19
14.00	ZP	3.94	32.1	4.52
Nov. 21, 1986, Outer Twin Bay, swarms				
15.30	HN	0.54	71.9	5.49
15.30	ZP	8.44	80.4	5.65
Feb. 21, 1987, The Lair, swarms				
10.45	HN	1.14	38.3	4.85
10.45	HN	0.94	38.0	4.83
10.45	ZP	2.82	66.5	5.43

stages, with lengths of 110–210 μm, as well as copepodid stages were collected with the 80 μm plankton net.

One hundred and twenty one samples (106 plastic bag, 8 sweep net and 7 plankton net) were collected. An entire sample or a subsample of 300 specimens was enumerated for adult sex and copepodid stage, which were separated by the number of swimming legs and/or urosome segments (F.D.Ferrari and J.W. Ambler, in preparation). An average copepodid stage for each sample was calculated as follows:

$$(1 \times CI + 2 \times CII + 3 \times CIII + 4 \times CIV + 5 \times CV + 6 \times CVI)/\text{total number}$$

This value could vary from 1.00 to 6.00. A sex ratio (percent males) was calculated for a sample as follows:

$$100 \times \text{number of adult males/number of adults}$$

Copepod densities in swarms estimated from the plastic bag samples were always higher than densities from samples collected with hand-held nets, but the two collection methods resulted in similar densities for samples of non-swarming

animals collected early in the morning (Table I). The average copepodid stage and percent adult copepods were similar for the two techniques.

During four of the trips (November 1986, July 1987, January 1988, June 1988), light intensity was measured *in situ* with an integrating quantum scalar irradiance meter (Biospherical Instruments Model QSI-140). This meter was held by hand for 2–5 min near or in a swarm, or in water from which pre-swarm or non-swarm samples were taken. Measurements of light intensity usually were made in the most accessible swarm.

More extensive sampling was carried out during January 1988 and June 1988. Copepod swarms were collected and light intensities measured at 15–30 min time intervals during three dawn and two dusk periods along the northern shore of outer Twin Bay. Flashlights covered with red cellophane were used for June 1988 observations during the early dawn, late dusk and night periods. Observations during earlier trips were made with uncovered dive lights. Mid-day measurements were also made during these trips.

Statistical tests were used from SAS version 5.16 on a VAX 11/750. Parametric statistics were used in correlation analyses of copepod density in swarms, light intensity and time of day. Four data sets were used: dawn and dusk periods sampled during several days in January 1988 and June 1988. Swarm samples were considered to be independent of one another. For seasonal comparisons of stage composition parameters, the Kruskal–Wallis nonparameteric rank sum test was used. Independence was assumed between swarm samples collected during the same season as well as from different seasons.

Generic designation

Dioithona oculata was previously reported as *Oithona oculata* or *Oithona* (*Dioithona*) *oculata*. In this paper we accept the generic name *Dioithona* for species of *Oithona* with two setae on the free segment of leg 5 (Kiefer, 1935). Morphological similarities and differences among species placed in the two genera continue to be documented (Nishida, 1985; Ferrari and Böttger, 1986). The appropriateness of this generic distinction has been discussed by Vervoort (1964) and Nishida (1985).

Results

Swarm description

Aggregations of diothonan copepods, mangrove mysids and planktivorous fishes were present under the canopy of red mangroves (Figure 3). Copepod swarms were usually observed around mangrove prop roots or close to tree trunks in water <1 m. Schools of the mangrove mysid, *Mysidium columbiae*, were also found around the outer submerged roots and branches. At the edge of the canopy, schools of anchovies (*Anchoa*), sardines (*Harengula*) and dwarf herrings (*Jenkinsia*) were often found during the day (Figure 3). At dusk, schooling fishes become more active and at night were not observed near the mangroves. Mysids remained around the mangrove roots throughout the night,
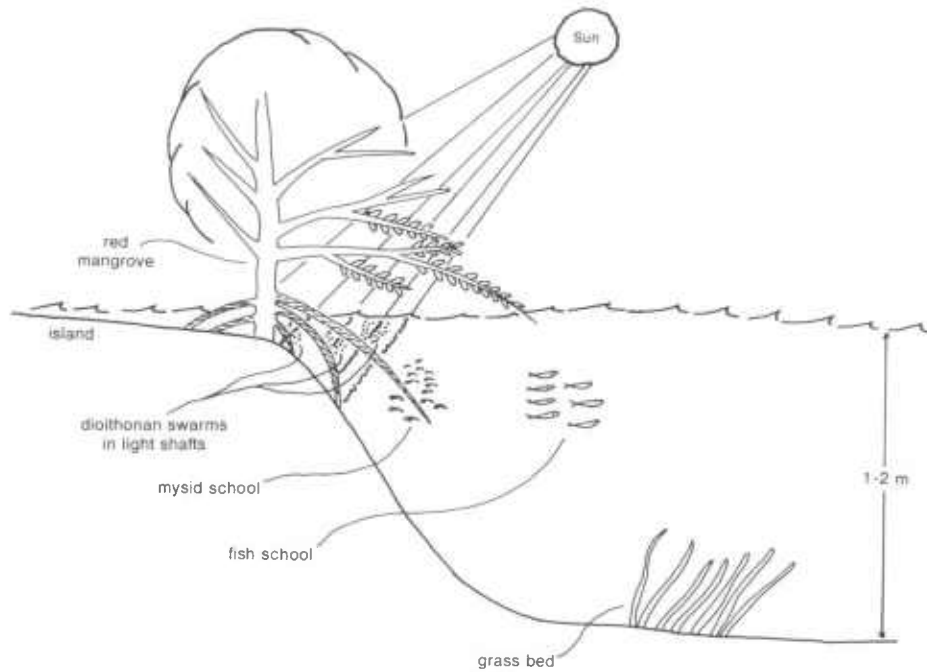
Fig. 3. Schematic of red mangrove (*Rhizophora mangle*) prop root habitat showing the location of the dioithonan (*D.oculata*) swarms, mysid schools (*M.columbiae*) and fish schools (*Anchoa*, *Harengula* and *Jenkinsia* species).

although their position in this habitat changed (Modlin, 1990). Dioithonan swarms dispersed at dusk, and were not seen again until ~1 h before sunrise. Swarms were not observed in open water or above turtle grass beds adjacent to the mangroves.

Dioithonan swarms were observed around mangrove prop roots in areas protected from prevailing weather during all trips, except March 1986 (Figure 2). Swarm size and position relative to mangrove prop roots appeared to be the same during each week-long observation period, but varied between trips. Small, cylindrical swarms (5–10 cm in diameter, 10–20 cm deep) were observed within light shafts which penetrated through the mangrove leaf canopy to the water. These small swarms usually were found among the prop roots in water <20 cm deep. Larger swarms extended beyond the light shaft edges. Occasionally these larger swarms were so numerous that discrete swarm units could not be distinguished and the swarms formed a layer or band parallel to the shore (November 1986 and July 1987). The largest continuous band was observed in February 1987 and extended ~1200 m from Twin Bays to a point opposite Lair Channel on the west shore of the Main Channel (Figure 2). North of this point discrete swarm units were observed. This band which occurred at the edge of the leaf canopy (away from the prop roots), differed markedly from the usual position of the smaller, discrete swarms.

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Population structure

Density and stage composition of *D.oculata* were determined near the mangrove prop roots and in the open water adjacent (3–5 m) to the mangroves during day and night (Figure 4). For the mangrove prop root habitat, six pairs of samples were collected during mid-day in swarms and in water immediately adjacent to
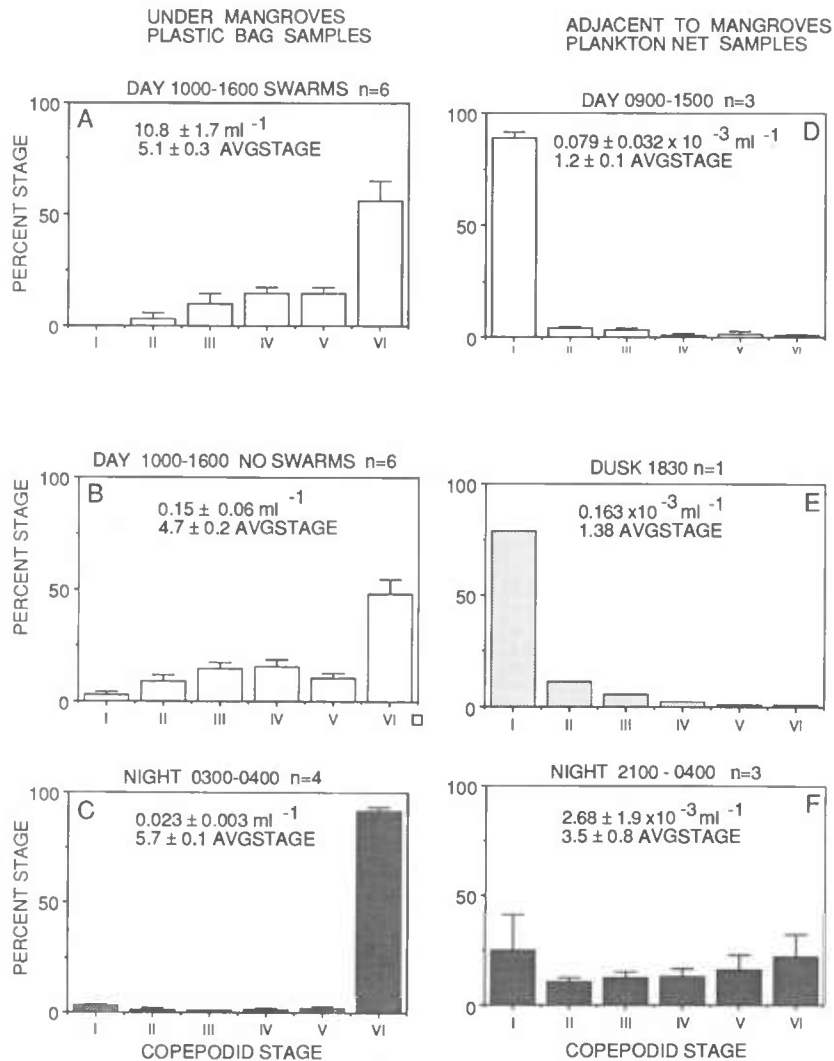

Fig. 4. Dioithonan copepodid stage distributions (CVI is adult) near the prop roots under the mangroves (A–C), and in open water adjacent to the mangroves (D–F). Also shown are mean ±SE for copepod density, and mean ±SE for average copepodid stage (AVGSTAGE). Samples were taken during the day (A, B and D), dusk (E), and night (C and F). Dates samples were taken: (A) June 1988 and May 1989; (B) June 1988 and May 1989; (C) June 1988; (D) October 1985 and February 1987; (E) November 1986; and (F) February 1987, October 1985 and July 1987. *n* = number of samples.

the swarms (Figure 4A and B). The mean density of the dioithonans in swarm samples was two orders of magnitude higher than the mean density of non-swarming animals, 10.8 ml^{-1} and 0.15 ml^{-1} respectively. Four samples of water were also collected near the mangrove roots at night when no swarms were present (Figure 4C). For all these samples, adult dioithonans dominated the stage composition, especially at night. Copepod densities were 2–3 orders of magnitude higher for swarming copepods than for non-swarming copepods.

Stage composition and density were dramatically different in the plankton samples collected 3–5 m away from the mangroves compared with the samples near the prop roots (Figure 4). For the plankton samples, copepodid stage one (CI) dominated during the day and at dusk, but no stage clearly dominated at night (Figures 4D–F). Densities of dioithonans in the plankton were 1–2 orders of magnitude lower than non-swarming dioithonans near mangrove prop roots, and 4–5 orders of magnitude lower than the swarming dioithonans. Plankton densities of dioithonans during the day were lower than those during night. Naupliar stages four–six were present in both day and night plankton tows.

All 95 swarms sampled for *D.oculata* contained adults (CVI), and almost all, 94 of 95 swarms, contained the oldest juvenile copepodid stages (CV and CIV). In 90 of the 95 swarms copepodid (CIII) were also present. Copepodid stages one and two (CI and CII) were found in 34 and 62% of the swarms respectively. Although females carrying egg sacs were present in the swarms, nauplii were never observed. Our laboratory observations indicate that dioithonan egg hatching usually occurs between 00.00 and 05.00 when copepods are dispersed from swarms into adjacent open waters (Ambler *et al.*, 1990). Nauplii are commonly collected in plankton net samples from open waters.

Swarm formation and dispersal

Light intensities measured in dioithonan swarms were plotted as a function of time of day for different months (Figure 5A). These light intensities showed significant linear relationships during the dawn and dusk periods in January 1988 (coefficient of correlation $r = +0.95$ and -0.94 respectively) and June 1988 ($r = +0.95$ and -0.86 respectively). The January and June 1988 data represent the seasonal extremes in light intensity: time of day is the same for both of these periods because daylight savings time is not observed in Belize.

Swarms collected in June 1988 formed earlier and dispersed later than those collected in January 1988 (Figure 5B). This shift coincided with the seasonal shift observed for light intensity in Figure 5(A). The earliest swarms were observed by 05.15 in the summer and by 06.00 in the winter at a mean light intensity of 13.82 ± 0.32 (SD) ($\log_{10}$ quanta cm^{-2} s^{-1}). These values were near the detection level of our irradiance meter. During dusk periods, swarms became fewer in number and more difficult to locate as light intensity decreased. Nevertheless some swarms were found at light intensities similar to the dawn threshold value.

For dawn periods in January and June 1988, copepod density in swarms increased with time of day but not as closely as light intensity (Figure 5). We observed significant coefficients of correlation (alpha <0.05) between copepod
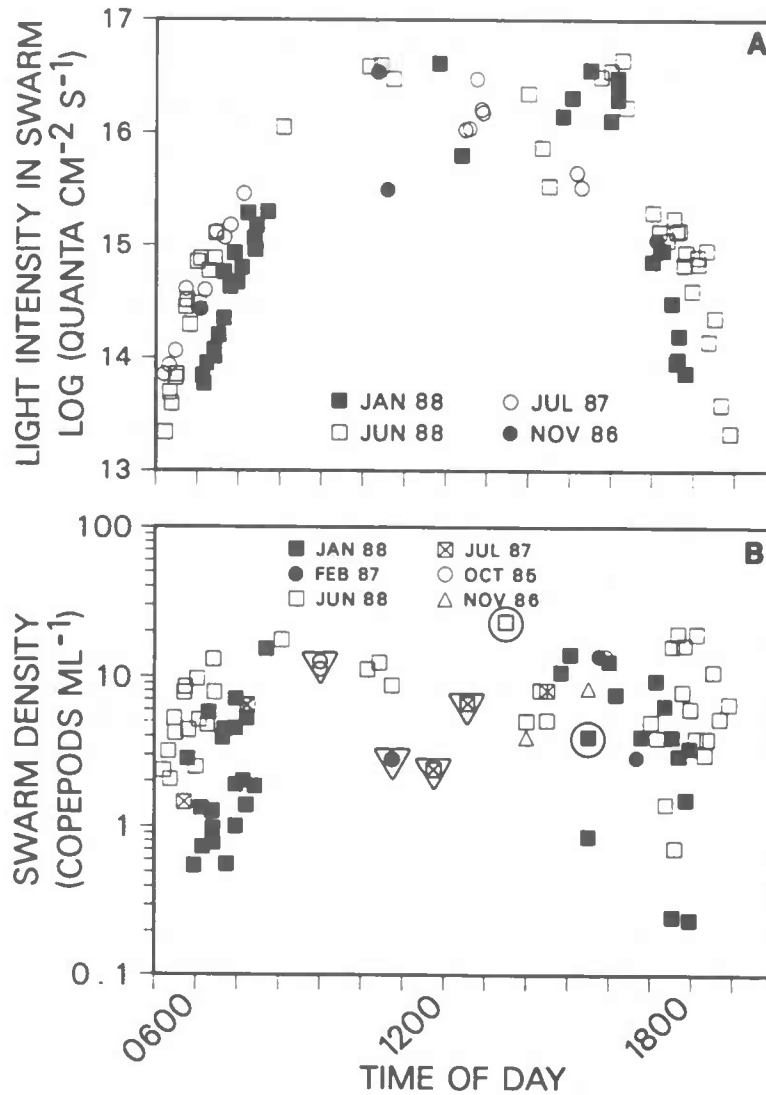
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Fig. 5. (**A**) Light intensity in dioithonan swarms measured *in situ* in outer Twin Bay. Swarms formed by 05.15 in June 1988 and by 06.00 in January 1988; swarms dispersed by 18.52 in June 1988 and 18.00 in November 1986. (**B**) Dioithonan density in swarms [$\log_{10}$ (density)] versus time of day for swarms collected in Twin Cays during six different months (October 1985, November 1986, February 1987, July 1987, January 1988 and June 1988). All swarms were collected in outer Twin Bay except those collected in (1) the Main Channel between the dock and the southern end of west Twin Cay (circle) and (2) the Lair and Lair Channel (triangle).

density in swarms and light intensity (January, $r = +0.49$; June, $r = +0.61$), and between copepod density in swarms and time (January, $r = +0.46$; June, $r = +0.64$). For January dusk, we also observed significant correlations of density with both light intensity ($r = +0.65$) and time ($r = -0.49$). Since light

intensity and time of sampling were highly correlated, we cannot distinguish between the relative contribution of these two potential influences on copepod density in swarms. Dusk periods during June were different. Copepod density in swarms was not significantly correlated with either light intensity or time of sampling.

Mid-day densities in swarms were similar during all trips and from several localities. The highest density, 23.2 copepods ml^{-1}, was recorded on the west side of the Main Channel during June 1988 (Figure 5). The mean density of dioithonans in a swarm was 9.1 ± 4.7 (SD) copepods ml^{-1} ($n = 17$) during mid-day, 08.00–16.30 (Figure 5). These dense swarms were usually observed in light shafts or well-lit areas, but were also found on cloudy days when there were no light shafts. The range of light intensity (log_{10} quanta cm^{-2} s^{-1}), measured during mid-day varied from 15.50 in shaded areas to 16.60 in the brightest areas which included shafts of light penetrating through the mangrove canopy (Figure 5). Samples of non-swarming dioithonans were collected in these shaded areas (Figure 4). At light intensities >16.03 (log_{10} quanta cm^{-2} s^{-1}), copepods in swarms did not disperse when the white Teflon sphere of the irradiance meter was held in the swarm. At lower light intensities, the swarming copepods moved away but quickly formed another swarm nearby.

Seasonal comparisons

Swarm composition parameters (percent adults, average copepodid stage and sex ratio) were compared between different months using a nonparametric rank sum test (Table II). Only mid-day samples from the different months were compared. The highest percent of adults, highest average copepodid stage and the lowest sex ratios occurred during summer (June and July).

A comparison between swarms collected in January and June 1988 revealed differences in copepod density in swarms, stage composition and sex ratio (Figure 6). These differences were all significant when tested with the Kruskal–Wallis nonparametric rank sum test. Fewer copepodid stages I and II and more adults were observed in June swarms than in the January swarms. Although densities in swarms were higher in June than January (Figure 5B), swarms in June were composed of larger older animals compared with swarms in January. A higher percentage of adults were females during June than January.

Discussion and conclusions

We report the first observations of *D.oculata* forming near-surface swarms among red mangrove roots. Hamner and Carleton (1979) also reported near-surface swarms in sea-level solution notches of limestone islands of Palau. Other workers have observed *D.oculata* swarms away from the surface in irregular masses or blanket swarms 10–50 cm above various substrates: white sand, corals, sea grasses and clearings within algal beds (Hamner and Carleton, 1979; Omori and Hamner, 1982; Ueda *et al.*, 1983), and within pockets or caves in coral reefs (Emery, 1968). The irregular ball-shaped swarms we observed near red mangrove roots generally were much smaller than those reported elsewhere;

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Table II. Comparison (Kruskal–Wallis nonparametric rank sum test) of swarm composition parameters for mid-day samples collected in different months

Month	n	% Adults	Sex ratio	Average copepodid stage
Jan. 1988	6	63.1	39.9	5.28
Feb. 1987	4	57.3	56.2	5.22
June 1988	9	76.9	29.5	5.51
July 1987	4	81.8	21.2	5.75
Oct. 1985	3	65.6	37.3	5.38
Nov. 1986	4	52.8	42.1	4.96
PROB>χ^{2a}		0.147	0.153	0.094

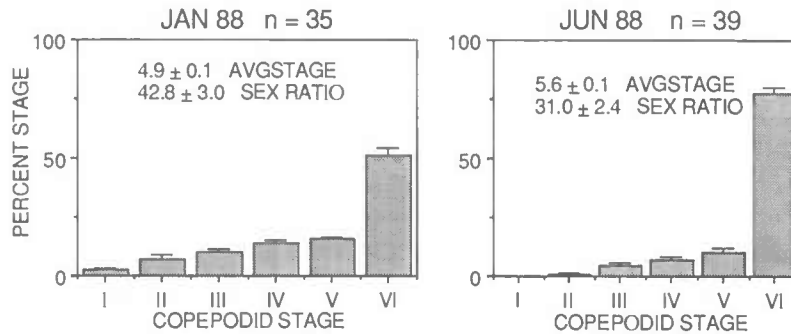[a] Probability of a greater chi square.

Fig. 6. Dioithonan copepodid stage distributions (CVI is adult) during different times of the day and different dates for the January and June 1988 trips. Also shown are mean ±SE for copepod sex ratio and mean ±SE for average copepodid stage (AVGSTAGE). All samples taken in Outer Twin Bay except one mid-day sample on June 4 and one on January 7 which were taken in the Main Channel. Three sweep net samples are included in June data. n = number of samples.

most other reports are of swarms ≥2 m in diameter. This difference in swarm size may result from the mangrove habitat which is broken up by prop roots and punctuated by shafts of light which have penetrated the overhead leaf canopy. We occasionally observed continuous bands of dioithonan swarms, but we did not see blanket swarms above nearby turtle grass beds or in the shallow ponds on Twin Cays. Hamner and Carleton (1979) stated that diothonan swarms, which are white, were difficult to see against white backgrounds of the solution notches. In the mangrove habitat the white swarms were easily visible in the light shafts, especially if females carried egg sacs with dark eggs. However, more careful observation was required to see swarms in shade.

Several techniques have been used to estimate densities in swarms (Table III). For all techniques, maximum densities in swarms were 1–2 orders of magnitude greater than densities of non-swarming copepods. Highest densities for swarming copepods have been obtained for *D.oculata* either by collection with small plastic bags (present study) or photographically by nearest-neighbor estimates (Hamner and Carleton, 1979). Ueda *et al.* (1983) obtained one high estimate of density in swarms for *Acartia sinjiensis* (reported as *A.plumosa*) by

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Table III. Estimates of density in swarms (mean ±SD) for copepods collected in different locations with different gear

Species	Sampling gear	*n*	Density (no. ml^{-1})
Emery (1968) Florida Keys			
Acartia spinata	Jars	1	0.110
Hamner and Carleton (1979) Great Barrier Reef, Australia			
Acartia australis	Diver-operated net	8	0.167 ± 0.041
A.australis	57 l plastic bag	1	0.210
A.australis	Photography	18	0.325 ± 0.087
A.australis	Photography	11	0.586 ± 0.193
Dioithona oculata[a]	Photography	14	1.558 ± 0.540
Ueda *et al.* (1983) Japanese temperate bays and subtropical reefs			
Acartia plumosa	Hand sweep net	1	2.000
A.steueri	Suction cylinder	8	0.070–0.500
A.clausi	Van Dorn sampler	1	0.300
Dioithona oculata[a]	Van Dorn sampler	1	0.400
Present study, Mangrove cays behind Belize Barrier Reef			
Dioithona oculata	Hand-held net	6	0.928 ± 0.026[b]
D.oculata	0.3–3.0 l bag	5	5.682 ± 2.497[b]
D.oculata	0.3–3.0 l bags	17	9.100 ± 4.700[c]

[a] *Dioithona oculata* is *Oithona oculata* in Hamner and Carleton (1979) and Ueda *et al.* (1983).
[b] From comparisons in Table I.
[c] Mid-day samples.

using a hand net and estimating total swarm volume. Most *Acartia* species had their highest densities of several hundred animals per liter compared with *D.oculata*, which had highest densities of several thousand per liter (Table III). Assuming isahedronic packing in a swarm (Hamner and Carleton, 1979), minimum nearest neighbor distance (center to center of copepod) in the present study would be 4.2 mm for our highest density of 23 copepods ml^{-1}. Adult females, which are the largest copepods in the swarms, have a maximum length of 0.80 mm (Ferrari and Bowman, 1980). The distance between copepods would then be less than five body lengths. The only observation of closer packing of copepods in an aggregation is for diapausing *Calanus pacificus californicus* in Santa Barbara Basin by Alldredge *et al.* (1984). Their observed minimum nearest-neighbor distance of 4.0 mm would result in distances between copepods of less than two body lengths.

In a study of swarms in Japan, Ueda *et al.* (1983) concluded that swarms were species specific. In only one location did they observe a swarm with two species of *Acartia*. Hamner and Carleton (1979) found only one mixed swarm composed of the mysid *Anisomysis pelewinsis* and the copepod *Centropages orsinii*. The mangrove swarms in our study were species specific, although occasionally the mangrove mysid, *M.columbiae*, could be seen swimming near dioithonan swarms.

Adult copepods often dominated swarms of *D.oculata*. Adults in the Japanese swarms ranged from 32 to 88%; in the 95 mangrove swarms we surveyed, the

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mean was $64.3 \pm 2.3\%$ (SE), with a range of 16.4–100%. In June, dioithonan swarms among mangrove roots in Twin Bays usually comprised CIV–CVI, while in January younger copepodids were more prevalent (Figure 6). However, younger copepodids were present in non-swarm samples from waters adjacent to swarms (see Figure 4A and B).

Females usually were more abundant than males in the mangrove swarms. We found a mean of $62.1 \pm 2.0\%$ (SE) of the adults were females in our 95 swarm samples but the range was very broad, 10.4–96.0%. The highest percentages of adult females usually occurred during the summer when densities were generally higher and when younger copepodids were absent from swarms. Therefore higher densities are not the result of closer packing of smaller animals, but may result from changes in population structure or behavior. Ueda *et al.* (1983) reported 80–100% of the adults were females in 28 out of 32 swarms containing *Acartia* species. They found lower percentages of adult females in their *D.oculata* swarms: 52.8–82.9%. Hamner and Carleton (1979) reported only slightly higher abundances of females than males for four swarms of *Acartia australis*.

Previous workers have inferred from plankton samples that swarms of *D.oculata* and several *Acartia* species occur only during the day (Hamner and Carleton, 1979; Omori and Hamner, 1982; Ueda *et al.*, 1983). Ueda *et al.* (1983) also reported from *in situ* observation that the number of swarms and copepod density in swarms were lower during the dawn and dusk periods than during mid-day. We have searched for swarms at night (between 19.00 and 04.00) for 6 h total on several trips to swarm habitats, but not observed any swarms. We have found that dioithonan density in swarms was only weakly correlated with light intensity during dawn when swarms are forming, and that densities in swarms typical of mid-day could be found within an hour of swarm formation (Figure 5). During dusk dispersal, densities in swarms decreased very rapidly and were either weakly or not correlated with light intensity. Swarm dispersal may appear to an observer to result from a decrease in the number of swarms along the shoreline as much as from decreasing copepod densities in swarms.

Our earliest observations of swarms during dawn occur at a mean threshold light intensity of 13.82 ($\log_{10}$ quanta cm^{-2} s^{-1}). At lower light intensities, densities of non-swarming dioithonans near prop roots were similar to those collected mid-day. This threshold light intensity may stimulate a photokinetic response at which the activity of the animals changes to aggregation. This response is similar to that observed to initiate vertical migration of some planktonic crustaceans (Forward *et al.*, 1984).

Our data suggest that population structure and density of *D.oculata* near mangrove prop roots and in open water adjacent to the mangroves were dramatically different during the day, and less so during the night. During the day, copepodid stage I (CI) and nauplii were found in open water adjacent to the mangroves, while the older copepodids were found in swarms near the prop roots. At night, the older copepodids were found in the plankton along with the CI and nauplii. Daytime swarm structure of dioithonans resembles that of some parasitic cyclopoid species which have free-swimming nauplii and copepod stage

I, and then infect their hosts as copepodid stage II (Dudley, 1966; Anderson and Rossiter, 1968) or copepodid stage III (Ooishi, 1980). For these cyclopoid species, young copepodids change their behavior after CI, and may co-occur with several older copepodids within the hosts (Heussner, 1983). This situation contrasts with free-living calanoid copepods, whose significant behavioral change occurs at CI and whose copepodid stages are often spatially assorted by depth (Ferrari, 1985; Ambler and Miller, 1987).

The most commonly suggested advantages of swarming are increased encounter for mating and avoidance of predators, which need not be mutually exclusive (Hamner and Carleton, 1979). Hebert *et al.* (1980) concluded that the main advantage of swarming for a freshwater predatory copepod was to increase mating encounters. Several studies (Alldredge *et al.*, 1984; Tanaka *et al.*, 1987a,b; Wishner *et al.*, 1988) observed extensive predation on swarming copepods, but did not evaluate whether swarming reduced this predation compared with non-swarming animals. In our study, the high percentage of adult dioithonans in the swarms may facilitate mating by placing potential mates in very close proximity. While we have observed the effects of predation on dioithonans in stomach contents of schooling fishes and mysids, we do not know to what extent these animals rely on dioithonans as prey. The effect of this predation on the present population structure of dioithonan swarms or the history of swarming also remains to be determined.

References

Alldredge,A., Robison,B., Fleminger,A., Torres,J., King,J. and Hamner,W. (1984) Direct sampling and *in situ* observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. *Mar. Biol.*, **80**, 75–81.
Ambler,J.W. and Miller,C.B. (1987) Vertical habitat-partitioning by copepodites and adults of subtropical oceanic copepods. *Mar. Biol.*, **94**, 561–577.
Ambler,J.W., Ferrari,F.D. and Fornshell,J.A. (1990) Diel cycles of egg production in copepods carrying egg sacs. *Eos*, **71**, 77.
Anderson,D. and Rossiter,G. (1968) Hatching and larval development of *Haplostomella australiensis* Gotto (Copepods, fam. Ascidicolidae), a parasite of the ascidian *Styela etheridgii* Herdman. *Proc. Linn. Soc. N.S.W.*, **93**, 464–475.
Dudley,P. (1966) Development and systematics of some Pacific marine symbiotic copepods. A study of the biology of the Notodelphyidae, associates of ascidians. *Univ. Wash. Pub. Biol.*, **21**, 1–202.
Emery,A. (1968) Preliminary observations on coral reef plankton. *Limnol. Oceanogr.*, **13**, 293–303.
Ferrari,F. (1985) Postnaupliar development of a looking-glass copepod, *Pleuromamma xiphias*

(Giesbrecht 1889), with analyses of distributions of sex and asymmetry. *Smithson. Contrib. Zool.*, **420**, 1–55.

Ferrari,F. and Bowman,T. (1980) Pelagic copepods of the family Oithonidae (Cyclopoida) from the east coasts of Central and South America. *Smithson. Contrib. Zool.*, no. 312.

Ferrari,F. and Böttger,R. (1986) Sexual dimorphism and a sex-limited polymorphism in the copepod *Parioithona pacifica* Nishida, 1985 (Cyclopoida: Oithonidae) from the Red Sea. *Proc. Biol. Soc. Wash.*, **99**, 274–285.

Forward,R.,Jr, Cronin,T. and Stearns,D. (1984) Control of diel vertical migration: photoresponses of a larval crustacean. *Limnol. Oceanogr.*, **29**, 146–154.

Hamner,W. and Carleton,J. (1979) Copepod swarms: attributes and role in coral reef ecosystems. *Limnol. Oceanogr.*, **24**, 1–14.

Haury,L., McGowan,J. and Wiebe,P. (1978) Patterns and processes in the time space scales of plankton distribution. In Steele,J. (ed.), *Spatial Patterns in Plankton Communities.* Plenum Press, New York, pp. 277–327.

Hebert,P., Good,A. and Mort,M. (1980) Induced swarming of the predatory copepod *Heterocope septentrionalis. Limnol. Oceanogr.*, **25**, 747–750.

Heussner,S. (1983) Parasitisme de *Pachypygus gibber* (Thorell, 1859), copépode ascidicole à deux formes mâles. Dynamique saisonniére de l'association avec l'hôte *Cione intestinalis* L. Hyothéses sur la determinisme sexual du parasite. These de 3éme cycle en Océanologie université d'Aix-maseille II.

Hirota,R. (1990) Microdistribution of the marine copepod *Oithona davisae* in the shallow waters of Ariake-kai mud flats, Japan. *Mar. Biol.*, **105**, 307–312.

Humes,A. and Smith,W. (1974) *Ridgewayia fosshageni* n. sp. (Copepoda; Calanoida) associated with an actiniarian in Panama, with observations on the nature of the association. *Carib. J. Sci.*, **14**, 125–139.

Kiefer,F. (1935) Zur kenntnis der Oithonidae (Crustacea Copepoda Cyclopoida). *Zool. Anz.*, **112**, 322–327.

Kimoto,K., Nakashima,J. and Morioka,Y. (1988) Direct observations of a copepod swarm in a small inlet of Kyushu, Japan. *Bull. Seikai Res. Fish. Lab.*, **66**, 41–58.

Mauchline,J. (1971) Seasonal occurrence of mysids (Crustacea) and evidence of social behavior. *J. Mar. Biol. Assoc. UK*, **51**, 809–825.

Modlin,R. (1990) Observations on the aggregative behavior of *Mysidium columbiae Mar. Ecol.*, *P.S.Z.N.*, **11**, 263–275.

Nishida,S. (1985) Taxonomy and distribution of the family Oithonidae (Copepoda Cyclopoida) in the Pacific and Indian Oceans. *Bull. Ocn. Res. Inst. Univ. Tokyo*, no. 20, 1–167.

Omori,M. and Hamner,W. (1982) Patchy distribution of zooplankton: behavior, population assessment and sampling problems. *Mar. Biol.*, **72**, 193–200.

Ooishi,S. (1980) The larval development of some copepods of the family Ascidicolidae, subfamily Haplostominae, symbionts of compound ascidians. *Pub. Seto Mar. Biol. Lab.*, **25**, 253–292.

Reutzler,K. and Feller,C. (1988) Mangrove swamp communities. *Oceanus*, **30**, 16–24.

Tanaka,M., Ueda, H. and Azeta,M. (1987a) Near-bottom copepod aggregations around nursery ground of the juvenile Red Sea bream in Shijiki Bay. *Nip. Suisan Gak.*, **53**, 1537–1544.

Tanaka,M., Ueda,H., Azeta,M. and Sudo,H. (1987b) Significance of near-bottom copepod aggregations as food resources for the juvenile Red Sea bream in Shijiki Bay. *Nip. Suisan Gak.*, **53**, 1545–1552.

Ueda,H., Kuwahara,A., Tanaka,M. and Azeta,M. (1983) Underwater observations on copepod swarms in temperate and subtropical waters. *Mar. Ecol. Prog. Ser.*, **11**, 165–171.

Vervoort,W. (1964) Free-living copepoda from Ifaluk Atoll in the Caroline Islands. *US Natl Mus. Bull.*, **236**, 121–431.

Wishner,K., Durbin,E., Durbin,A., Macaulay,M., Winn,H. and Kenney,R. (1988) Copepod patches and right whales in the Great South Channel off New England. *Bull. Mar. Sci.*, **43**, 825–844.

Yeatman,H. (1969) A redescription of copepod, *Ridgewayia marki* with description of an unusual specimen. *J. Tenn. Acad. Sci.*, **44**, 7–10.