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Emergent zooplankton in Moreton Bay, Queensland, Australia: seasonal, lunar, and diel patterns in emergence and distribution with respect to substrata

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ABSTRACT: Forty-three putative taxa were common in emergence trap, re-entry trap, and net tow samples taken in Moreton Bay, Queensland, Australia between 20 January and 14 February and between 14 July and 23 August 1985. Twenty-nine taxa were composed of adults with 17 groups classified as demersal zooplankters. The remaining 14 taxa consisted of early life history stages. Statistically significant factorial variations in numbers of zooplankters captured were found between seasons (2 to 500), among lunar periods (2 to 150), and among substrata (2 to 200). Summer samples yielded greater numbers of 25 of the 32 taxa composed of adults and 10 of the 14 larval groups. Ten of the 17 demersal taxa, 5 other groups of adults, and 5 larval forms emerged in greater numbers during either lunar quarter or the new moon. Significant emergence during full moons was observed for 9 of the 14 larval taxa, 5 demersal groups, and 5 other adult taxa. Forty-one out of the 43 taxa emerged in statistically greater numbers from 1 of the 2 more complex substrata, coral or seagrass, as compared to mud or coral rubble. Five different temporal emergence patterns were displayed by 34 taxa with most emergence occurring at night.

INTRODUCTION

Studies of zooplankton that associate with the substratum during the day and enter the water column at night have been centered on coral reefs. These investigations often involved the use of emergence or re-entry traps to capture migrating zooplankters. Numbers of animals captured varied with seasons, lunar periods, substratum types, and time of day (Alldredge & King 1977, Porter & Porter 1977, Porter et al. 1977, Feeley et al. 1979, Hobson & Chess 1979, McWilliam et al. 1981, Walter et al. 1981, Ohlhorst 1982, Jacoby & Greenwood 1988). Further use of these methods has identified noctural migrations of zooplankters from subtidal sand flats (Alldredge & King 1980, 1985, Youngbluth 1982a, Stretch 1985), seagrass beds (Robichaux et al. 1981, Alldredge 1985, Bell et al. 1986, Hicks 1986, Walters & Bell 1986), kelp beds (Hammer & Zimmerman 1979, Hammer 1981), and a variety of substrata in a temperate estuary (Thomas & Jelley 1971).

Demersal zooplankton, i.e. animals that regularly migrate into the water column at night from a daytime position in, on, or near the substratum, initially became of interest as a part of the trophic webs of coral reefs (Johnson 1949, Emery 1968, Hamner & Carleton 1979). Members of this assemblage currently are considered an important food source for invertebrates and fishes in a variety of habitats (Porter 1974, Hobson & Chess 1976, 1978, Robertson & Howard 1978, Nelson 1979, Alheit 1981, Alheit & Scheibel 1982, Choat 1982, de Morais & Bodiou 1984, Leber 1985). Estuaries represent nursery grounds for many fishes and invertebrates (McHugh 1967), therefore, demersal zooplankton in estuaries should represent a critical link to higher trophic levels.

This study was designed to examine behavior and distribution of demersal zooplankton in Moreton Bay, a subtropical estuary on the east coast of Australia. Reentry traps, net tows, and 2 types of emergence traps were used to characterize the zooplanktonic community. Analyses focused on variations in numbers of zoo-

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plankters captured from different substrata during different seasons, lunar periods, and times of day.

MATERIALS AND METHODS

General sampling procedure. Sampling was conducted at 2 locations in Moreton Bay (27° 20′ S; 153° 15′ E) southeast of Brisbane, Queensland, Australia. One locale was off Polka Point on the west side of North Stradbroke Island in 0.7 to 2.5 m of water with muddy sand (mud) or seagrass (grass) substratum. The second location had coral patches (coral) and a coral rubble (rubble) substratum in 0.7 to 3.5 m of water and was located along the east side of Goat Island ca 2.5 km southwest of Polka Point. Because the locations were subject to similar hydrological conditions, samples were attributed to 1 of the 4 substrata. It was recognized that other site-specific phenomena may have influenced the numbers of zooplankters captured.

Samples were taken between 20 January and 14 February and between 14 July and 23 August 1985. These periods represented the extremes in hydrological conditions and daylength. Salinity in Moreton Bay typically ranges from 34 ‰ in summer to 28 ‰ in winter (Newell 1971). A summer to winter decrease in water temperature from 25 to 13 °C was recorded at both sites. Daylength was 13.5 h in summer and 10.5 h in winter. Comparisons were made between these 2 seasonal extremes although it was acknowledged that factors specific to the year 1985 may have altered the numbers of zooplankters captured.

Three types of sampling were used to characterize the distributions and behavior of zooplankton. A plankton net was towed at the surface during daytime and night-time to estimate the number and diversity of zooplankters reaching the upper 0.5 m of the water column. Re-entry traps were used to determine the abundance and diversity of zooplankters near the bottom during the day. Zooplankters migrating from near the bottom into the water column were captured in 2 types of emergence traps.

Net tows. A 200 µm mesh plankton net with a 40 cm mouth was towed within 0.5 m of the surface during new moons. Night tows were made at 20:00 h on 24 January and at 19:30 on 19 July. Daytime samples were taken at 08:00 on 25 January and at 13:30 h on 19 July. A General Oceanics 2030 flowmeter attached to the net provided data needed to calculate the volumes of water filtered during the 5 min tows. All plankton net tows were made at the Polka Point site in ca 1.5 m of water These and all other samples were concentrated on a 100 µm mesh sieve and preserved in 4 % formaldehyde in seawater.

Re-entry traps. These consisted of 19.5 × 26 cm (0.051 m^2) plastic trays that were 8.5 cm deep and could be sealed (Jacoby & Greenwood 1988). The trays contained 5 to 7 cm of muddy sand from the Polka Point site. The sediment had been rinsed 10 times with freshwater to remove zooplankters and air-dried prior to deployment. Six traps were filled with filtered seawater, covered, and anchored on seagrass at the Polka Point site at 17:00 h on 11 February (last lunar quarter) and at 11:30 h on 15 July (new moon). All 6 trays were opened to permit colonization. Two traps were covered and retrieved between 08:30 and 09:00 h after each of 3 consecutive nights. A maximum of 1500 ml of non-interstitial water was collected in each trap. Zooplankters were rinsed from the sediment with freshwater 5 times onto a 100 µm sieve and then preserved. Trays were located on grass to ensure that colonizers had to move from the adjacent mud substratum to locate the available space. All comparisons were limited to samples taken from mud.

Net emergence traps. Four emergence traps made of 100 µm mesh (net traps; Jacoby & Greenwood 1988) were placed over 1 m^2 patches of each substratum at each site for 3 nights during new moon periods in summer and winter. A total of 8 net traps were deployed over grass and mud substrata at Polka Point on 20, 24, and 25 January and on 16, 17, and 19 July. Four net traps were set above coral and 4 traps were placed on rubble at Goat Island on 21, 22, and 23 January and on 14, 15, and 18 July. Coral and grass substrata were not composed of a single type of bottom. Coral formations had to be less than 1 m^2 and 50 cm high to fit under the traps; therefore, net traps deployed over coral also covered some rubble. Seagrass at Polka Point grew from a muddy sand substratum similar to bare mud. Net traps were deployed between 14:30 and 15:30 h, and were retrieved between 08:30 and 09:30 h the next morning. The resulting 18 h sampling period was treated as 1 night in analysis of seasonal and substratum-related differences in emergence. Samples were concentrated and preserved as described previously

Rotary emergence traps. A second type of emergence trap, rotary emergence trap (RET; Youngbluth 1982a, b, Jacoby & Greenwood 1988), was set over 1 m^2 patches of grass and mud at the Polka Point site and over small coral formations off Goat Island. Once again, patches of coral and grass were not pure substrata. Two RETs were placed over each of the 3 types of bottom for 1 night during each lunar period in summer and winter Sampling began between 14:30 and 15:30 h and ended between 11:30 and 12:30 h the following day. Fourteen separate samples of 90 min duration were taken during this 21 h period because the RETs have multiple cod ends which rotated into position to sample for a pre-set time interval. The 14 samples were treated as indicating time of first emergence to ca 70 cm (the point where zooplankters were trapped in the cod ends), and data from these samples were used in analyses of temporal patterns in emergence. Counts from all 14 samples were summed to yield numbers m^{-2} $night^{-1}$ which were analysed for seasonal, lunar, and substratum-related differences in emergence. Samples were sieved and concentrated as described above.

Analyses of samples and data. Zooplankters in all samples were identified and enumerated using a dissecting microscope. In general, full samples were counted, but extremely abundant taxa were counted in subsamples taken with a Stempel pipette. Only putative taxa taken with sufficient frequency to allow statistical analyses of their distributions were included.

Within each season, chi-square contingency tests (Zar 1974) were used to examine variation in the numbers of zooplankters captured among the 5 different types of samples and between daytime and night-time net tows. For summer data, mean numbers of zooplankters captured m^{-2} $night^{-1}$ in re-entry traps during the last quarter were compared to mean numbers m^{-2} $night^{-1}$ captured from mud by net traps and RETs during the new moon and to numbers m^{-3} taken in daytime and night-time net tows during the new moon. A similar comparison was made using winter data except that all 5 types of sampling were done during the new moon. Numbers of zooplankters m^{-3} taken in daytime and night-time net tows also were compared separately for each season.

Seasonal, exposure-related, lunar, substratum-related, and diel variations in numbers of zooplankters captured by re-entry and emergence traps were examined using analyses of variance (ANOVAs) (SAS Institute Inc. 1985) and a posteriori Student-Newman-Keuls multiple comparison tests (S-N-K tests). Factors were considered fixed because a majority of all possible levels were represented in the analyses. Cochran's test was used to detect heterogeneity of variances prior to ANOVAs (Underwood 1981). Data typically were heteroscedastic with variances proportional to the means, so counts (c) were log (c + 1) transformed prior to analysis. Variances of some data sets remained heterogeneous; therefore, outlying data points were replaced with values equal to or proportional to the mean of the data set. This procedure reduced variance without altering the means. Degrees of freedom were removed from mean squares as appropriate (Underwood 1981). Significance levels were held at $p < 0.05$ or $p < 0.01$.

RESULTS

General results

Samples yielded 43 common, putative taxa. Taxonomic divisions varied from separate age and sex groups within a species to broad categories at the class level. Effort was concentrated on relatively common and numerous groups which were prospective demersal zooplankters; however results for all common taxa were included to illustrate contrasts in behavior and distribution.

Numbers of all taxa varied greatly among replicate samples suggesting spatially and temporally patchy distributions. Outliers were replaced in most ANOVAs. This procedure may have increased Type I error; therefore, caution was used when considering results. In general, only one replacement was made for any taxon in an analysis. Furthermore, the total number of outliers replaced never exceeded 1 % of the data, and the total number of non-zero outliers never exceeded 0.7 % of the data. Variability was most extreme for adult copepods and copepodites in the calanoid genus *Acartia* (up to 900 times and 65 times respectively), polychaetes (up to 71 times), and caridean/anomuran larvae (up to 21 times).

Comparisons among samplers

Comparisons of the 5 types of sampling were restricted to results from mud. They revealed that the number of zooplankters captured within each season and taxon was not independent of trap type (Summer: chi-square = 83297.2, Df = 148, $p < 0.001$; Winter: chi-square = 17490.4, Df = 120, $p < 0.001$). Within each season and taxon, the mean numbers of zooplankters captured m^{-2} or m^{-3} were summed across all 5 types of samples. This sum was used as the denominator for calculations of the percentage contribution by each type of sampling (Table 1). Twenty-five of the 38 taxa analysed were taken predominately in re-entry or emergence traps. A total of 13 taxa were reasonably common in net tows with 5 groups more numerous in night-time tows and 8 taxa occurring in approximately equal numbers in daytime and night-time net tows.

Four other taxa were too rare in the appropriate sample sets to be included in the analyses. Examination of all available data indicated that tunicate larvae and calanoid copepods in the genera *Pseudocyclops* and *Ridgewayia* were taken in greatest numbers in emergence traps. Isopods were captured mainly in emergence and re-entry traps. Some taxa absent from net tows, e.g. copepod nauplii, miscellaneous nauplii, and tunicate larvae, were too small to be sampled quantitatively by the 200 µm mesh net.

Net tow data

Numbers of zooplankters m^{-3} taken in net tows within each season and taxon were not independent of the time of the tow (Summer: chi-square = 256.2, Df =

Table 1. Distribution of zooplankton captures by type of trap. Within a season, mean numbers of zooplankton m^{-2} or m^{-3} are not independent of taxon or type of trap as shown by chi-square contingency analyses ($p < 0.05$). Underlined percentages are at least 50 % of the summed means within taxon and season and are considered significant. NA: summed means < 19; cop.: copepodites

Taxon/season	Sum of means	Percent of summed means: Re-entry trap	Emergence traps: Net	Emergence traps: RET	Tows: Night	Tows: Day
Re-entry > Emergence > Tows						
Pseudodiaptomus colefaxi cop.						
Summer	412	87.1	0.8	7.5	2.7	1.9
Winter	140	60.7	9.3	28.6	1.4	0
Peltidium spp.						
Summer	50	72.0	8.0	20.0	0	0
Winter	56	87.5	5.3	3.6	1.8	1.8
Amphipods						
Summer	491	91.9	1.8	5.7	0.6	0
Winter	753	85.0	3.3	10.9	0.8	0
Cumaceans						
Summer	309	96.1	1.0	2.3	0.3	0.3
Winter	583	98.1	0.3	1.4	0.2	0
Ostracods						
Summer	1660	81.8	0.7	17.2	0.2	0.1
Winter	230	91.0	6.5	1.7	0.4	0.4
Polychaetes						
Summer	248	79.0	6.5	12.1	1.6	0.8
Winter	56	58.9	10.7	28.6	1.8	0
Gastropods						
Summer	407	67.3	11.6	21.1	0	0
Winter	69	75.4	10.2	11.6	1.4	1.4
Re-entry = Emergence > Tows						
Pseudodiaptomus colefaxi ♂♂						
Summer	285	80.4	9.1	7.7	1.8	1.0
Winter	132	34.9	24.2	39.4	1.5	0
Pseudodiaptomus colefaxi ♀♀						
Summer	133	66.2	3.0	19.5	8.3	3.0
Winter	135	41.5	5.2	50.4	2.2	0.7
Pseudodiaptomus colefaxi ovigerous ♀♀						
Summer	32	72.0	9.0	7.0	9.0	3.0
Winter	47	27.7	40.4	29.8	2.1	0
Oithona spp.						
Summer	6859	66.8	1.0	25.1	4.5	2.6
Winter	861	36.2	5.5	51.6	5.6	1.1
Miscellaneous harpacticoids						
Summer	61463	92.5	0.6	6.7	0.1	0.1
Winter	3592	47.7	6.7	44.9	0.6	0.1
Copepod nauplii						
Summer	4759	53.3	2.2	44.5	0	0
Winter	3940	7.7	8.3	84.0	0	0
Cirripede larvae						
Summer	161	59.0	3.1	17.4	9.3	11.2
Winter	111	11.7	28.8	54.1	4.5	0.9
Tanaids						
Summer	28	36.0	11.0	43.0	7.0	3.0
Winter	46	56.5	2.2	41.3	0	0
Polychaete larvae						
Summer	222	42.8	4.5	45.0	3.6	4.1
Winter	201	16.4	10.5	70.6	2.0	0.5
Mysids						
Summer	102	45.1	2.9	37.3	14.7	0
Winter	94	38.3	3.2	46.8	11.7	0
Re-entry = Night tow > Emergence						
Carideans						
Summer	22	27.0	5.0	9.0	41.0	18.0
Winter	9	NA				
Emergence > Re-entry = Tows						
Stephos spp.						
Summer	33	9.1	3.0	78.8	3.0	6.1
Winter	19	0	42.1	57.9	0	0
Parvocalanus sp.						
Summer	165	1.8	4.8	75.8	9.7	7.9
Winter	172	0.5	2.8	87.8	6.6	2.3
Parategastes sp.						
Summer	442	2.9	6.1	90.3	0.5	0.2
Winter	833	24.7	6.4	68.6	0.2	0.1
Miscellaneous nauplii						
Summer	28	0	7.0	93.0	0	0
Winter	47	6.4	2.1	91.5	0	0
Zoeae						
Summer	62	0	22.6	59.7	12.9	4.8
Winter	86	0	1.2	55.8	4.6	38.4

Table 1 (continued)

Taxon/season	Sum of means	Re-entry trap	Percent of summed means Emergence traps Net	RET	Tows Night	Day
Emergence > Re-entry = Tows						
Metis holothuriae						
Summer	66	15.2	3.0	75.8	1.5	4.5
Winter	6	NA				
Caridean/anomuran larvae						
Summer	91	0	12.1	76.9	7.7	3.3
Winter	7	NA				
Spadella cephaloptera						
Summer	34	8.8	3.0	88.2	0	0
Winter	1	NA				
Emergence = Night tow > Re-entry						
Megalopa						
Summer	41	7.3	4.9	9.8	70.7	7.3
Winter	26	0	3.8	69.2	26.9	0
Larvaceans						
Summer	170	5.9	5.9	21.2	51.7	15.3
Winter	1579	0.2	1.3	97.5	0.9	0.1
Gastropod veligers						
Summer	4477	4.8	1.5	3.4	60.7	29.6
Winter	485	2.1	10.5	76.7	9.9	0.8
Bivalve veligers						
Summer	1123	0.5	27.3	39.4	28.5	4.3
Winter	2262	0	41.4	58.1	0.4	0.1
All trap types approximately =						
Acartia spp. adults						
Summer	315	20.7	5.4	10.1	29.5	34.3
Winter	1049	19.4	4.5	66.7	5.2	4.2
Acartia spp. cop.						
Summer	546	13.2	4.8	45.8	20.1	16.1
Winter	2151	3.8	4.5	86.4	3.3	2.0
Calanoid cop.						
Summer	800	16.7	1.4	30.5	25.6	25.8
Winter	1689	2.1	2.0	76.2	10.4	9.3
Miscellaneous cyclopoids						
Summer	307	24.4	2.3	16.4	26.1	30.3
Winter	420	10.0	1.0	82.6	5.0	1.4
Miscellaneous calanoids						
Summer	498	17.1	2.0	8.0	44.0	28.9
Winter	217	15.2	2.8	3.7	43.3	35.0
Pseudodiaptomus mertoni adults						
Summer	42	14.3	11.9	19.0	31.0	23.8
Winter	12	NA				
Pseudodiaptomus mertoni cop.						
Summer	83	3.6	2.4	45.8	29.9	19.3
Winter	3	NA				
Sagitta spp.						
Summer	196	11.8	1.0	16.8	32.1	38.3
Winter	11	NA				

22, $p < 0.001$; Winter: chi-square = 114.7, Df = 12, $p < 0.001$). Comparisons of the proportions of zooplankters captured at night and during the day (Table 2) revealed that only zoeae were more common in any of the daytime net tows. In contrast, 10 groups of zooplankters were consistently more numerous in night-time net tows. A further 12 taxa were captured in approximately equal numbers in daytime and night-time tows.

The remaining 19 taxa were too rare to be included in the analyses (total numbers taken less than 19 m^{-3} in all tows). Examination of the data for males and ovigerous females of the calanoid *Pseudodiaptomus colefaxi*, the harpacticoid *Parategastes* sp., amphipods, cumaceans, ostracods, tanaids, and polychaetes revealed that they were captured only in night tows. A harpacticoid, *Metis holothuriae*, was taken in both daytime and night-time tows. Calanoids in the genera *Stephos*, *Pseudocyclops*, and *Ridgewayia*, as well as copepod nauplii, isopods, miscellaneous nauplii, the chaetognath *Spadella cephaloptera*, gastropods, and tunicate larvae, were extremely rare in all tows.

Re-entry trap data

ANOVAs applied to re-entry trap data indicated a significant effect due to season, night, and taxon (Cochran's value unadjusted = 0.06, Df = 1,252, $p < 0.05$; Cochran's value adjusted = 0.03, $p > 0.05$, loss of 2 Df; $F = 1.94$, Df = 82,250, $p < 0.001$). S-N-K tests (SE = 0.36) comparing abundances among the 42 taxa within each season and night indicated that miscellaneous harpacticoid copepods were the only zooplankters consistently captured in significantly greater numbers.

Table 2. Distribution of zooplankton captures in surface net tows. Within a season, mean numbers captured m^{-3} are not independent of time of day as shown by chi-square contingency analyses ($p < 0.05$). Underlined percentages are over 60 % of the grand mean within a season and are considered significant. NA: number m^{-3} < 10; cop.: copepodites

Taxon	Summer			Winter		
	Total no.	% of mean		Total no.	% of mean	
		Night	Day		Night	Day
Day > Night						
Zoeae	11	73	27	37	11	89
Night > Day						
Gastropod veligers	4043	67	33	52	92	8
Oithona spp.	484	63	37	58	83	17
Bivalve veligers	368	87	13	10	90	10
Larvaceans	114	77	23	16	88	12
Miscellaneous harpacticoids	100	64	36	25	88	12
Mysids	15	100	0	11	100	0
Megalopa	32	91	9	7	NA	NA
Pseudodiaptomus colefaxi ♀♀	15	73	27	4	NA	NA
Carideans	13	69	31	1	NA	NA
Caridean/anomuran larvae	10	70	30	4	NA	NA
Day = Night						
Calanoid cop.	411	50	50	332	53	47
Miscellaneous calanoids	363	60	40	170	55	45
Acartia spp. adults	201	46	54	99	56	44
Acartia spp. cop.	198	56	44	114	62	38
Miscellaneous cyclopoids	173	46	54	27	78	22
Parvocalanus sp.	29	55	45	51	75	25
Sagitta spp	138	46	54	9	NA	NA
Pseudodiaptomus mertoni adults	23	56	44	2	NA	NA
Pseudodiaptomus mertoni cop.	40	60	40	2	NA	NA
Cirripede larvae	33	45	55	6	NA	NA
Pseudodiaptomus colefaxi cop.	19	58	42	2	NA	NA
Polychaete larvae	17	47	53	5	NA	NA

Further multiple comparison tests revealed few significant differences among numbers of zooplankters captured m^{-2} among the 3 nights of exposure to colonization (Table 3). Differences were observed in 5 of the 42 taxa, but there was no consistent relation between changes in numbers captured and increased exposure.

Seasonal patterns in re-entry trap data were indicated by S-N-K tests for 19 out of 42 taxa (Table 4). Fifteen groups were taken in greater numbers during the summer. *Acartia* spp. adults and copepodites, as well as *Parategastes* sp., were more numerous in winter samples. Miscellaneous cyclopoid copepods, a broad taxon, did not display a consistent seasonal trend. Twenty-three taxa were captured in statistically equal numbers in both seasons.

Net emergence trap data

A significant interaction between season, substratum, and taxon was revealed by ANOVA applied to net emergence trap data (Cochran's value unadjusted = 0.04, Df = 11,336, $p < 0.05$; Cochran's value adjusted = 0.009, $p > 0.05$, loss of 45 Df, $F = 7.36$, Df = 123,3651, $p < 0.0001$). S-N-K tests comparing numbers of zooplankters emerging m^{-2} night^{-1} among the 42 taxa within each level of season and substratum (SE = 0.09) revealed that cyclopoid copepods in the genus *Oithona*, miscellaneous harpacticoid copepods, copepod nauplii, and bivalve veligers were the only groups regularly captured in statistically greater numbers.

Thirty-six of the 42 taxa exhibited significant seasonal differences in numbers captured in net traps (Table 5). Eighteen groups were more numerous in summer samples, and 17 taxa were taken predominantly in winter samples. Miscellaneous calanoid copepods were captured in statistically greater numbers in both seasons depending upon the substratum sampled. *Pseudocyclops* spp., *Metis holothuriae*, carideans, isopods, *Spadella cephaloptera*, and tunicate larvae were captured in statistically equal numbers from all substrata in both seasons.

Comparisons of emergence into net traps from different substrata within season and taxon indicated that 22 taxa emerged in significantly greater numbers from one of the 2 structurally complex substrata (coral or grass) either alone or in combination with one of the simple substrata (rubble or mud) (Table 6). A total of 10 taxa displayed significant differences in emergence but did not exhibit a clear pattern with regard to type of bottom. Copepodites of the calanoid *Pseudodiaptomus mertoni*, *Pseudocyclops* spp., copepod nauplii, carideans, caridean/anomuran larvae, miscellaneous nauplii, *Spadella cephaloptera*, chaetognaths in the genus *Sagitta*, gastropod veligers, and tunicate larvae emerged in statistically equal numbers from all 4 substrata.

Table 3. Taxa displaying significant differences in numbers captured in re-entry traps among nights of exposure. Values are mean nos. m^{-2} ($n = 4$); means are back-transformed from log ($c + 1$); underlined means are significantly greater within taxon and season (ANOVA and S-N-K tests, $p < 0.05$)

Taxon/season	Night 1	Night 2	Night 3
Acartia spp. adults			
Summer	0	124.0	62.1
Winter	399.2	92.3	5.3
Acartia spp. copepodites			
Summer	0	180.9	0
Miscellaneous calanoids			
Winter	56.0	0	3.5
Oithona spp.			
Summer	323.7	7004.2	5433.9
Miscellaneous cyclopoids			
Summer	67.9	151.9	0

Pooled rotary emergence trap data

ANOVA applied to RET data that had been summed across the 14 sampling intervals indicated a significant interaction effect due to season, lunar period, substratum, and taxon (Cochran's value unadjusted = 0.023, Df = 1,1032, $p < 0.05$; Cochran's value adjusted = 0.0113, $p > 0.05$, loss of 12 Df; $F = 2.32$, Df = 252,1020, $p < 0.001$). Of the 43 taxa included in the analysis, only *Oithona* spp., miscellaneous harpacticoids, copepod nauplii, and bivalve veligers were consistently taken in greater numbers as shown by S-N-K multiple comparisons (SE = 0.15).

S-N-K tests among mean numbers of zooplankters emerging m^{-2} $night^{-1}$ revealed significant seasonal differences for all 43 taxa (Table 7), significant lunar differences for 40 groups (Table 8), and significant substratum-related differences for 42 taxa (Table 9). Summer increases in emergence were observed for 25 taxa, and winter increases in numbers were indicated for 7 taxa. Eleven groups did not display a consistent seasonal pattern. Fifteen taxa emerged in statistically greater numbers in either lunar quarter or the new moon, that is during lunar periods in which at least part of the night is moonless. Another set of 15 taxa displayed significantly greater emergence during full moons and no more than 2 of the other 3 lunar periods. Ten of the remaining 13 groups were captured in significantly greater numbers in each of the 4 lunar periods depending upon the season and substratum sampled. *Oithona* spp., miscellaneous harpacticoids, and gastropods emerged in statistically equal numbers during all lunar periods. Samples taken over coral and grass yielded greater numbers of 24 taxa, and a further 10 groups emerged in greater numbers from either complex substratum in combination with mud. Eight taxa did not display a consistent substratum-related pattern in emergence, and copepod nauplii emerged in statistically equal numbers from all types of bottom.

Table 4. Taxa displaying significant seasonal differences in numbers captured in re-entry traps. Values are mean nos. m^{-2} ($n = 6$); means are back-transformed from log ($c + 1$); underlined means are significantly greater within taxon and night (ANOVA and S-N-K tests, $p < 0.05$). cop.: copepodites

Taxon/night	Season: Summer	Season: Winter
Summer > Winter		
Pseudodiaptomus colefaxi ♂♂		
Night 2	352.4	27.8
Night 3	196.1	3.5
Pseudodiaptomus colefaxi ovigerous ♀♀		
Night 2	27.8	0
Pseudodiaptomus colefaxi cop		
Night 3	435.8	27.8
Miscellaneous calanoids		
Night 2	155.6	0
Night 3	58.8	3.5
Calanoid cop		
Night 2	277.4	19.6
Night 3	87.7	5.3
Oithona spp.		
Night 2	7004.2	391.0
Night 3	5433.9	131.6
Miscellaneous harpacticoids		
Night 2	69168.7	1898.9
Night 3	85053.7	1358.5
Copepod nauplii		
Night 2	3594.2	68.8
Night 3	3185.9	87.7
Ostracods		
Night 3	2152.5	138.7
Cirripede larvae		
Night 1	166.4	5.3
Night 2	44.2	0
Polychaetes		
Night 3	260.1	3.5
Polychaete larvae		
Night 3	194.1	5.3
Sagitta spp.		
Night 2	39.2	0
Night 3	19.6	0
Gastropods		
Night 1	447.5	5.3
Gastropod veligers		
Night 1	39.4	0
Night 2	348.0	3.5
Night 3	133.8	5.3
Winter > Summer		
Acartia spp. adults		
Night 1	0	399.2
Acartia spp. cop.		
Night 1	0	89.0
Parategastes sp		
Night 1	5.3	75.9
Night 2	0	136.0
Night 3	19.6	232.6
Summer = Winter		
Miscellaneous cyclopoids		
Night 1	67.9	5.3
Night 3	0	48.0

Unpooled rotary emergence trap data

Forty-three separate ANOVAs, one per taxon, were used to analyse unpooled RET data. A total of 34 taxa

Table 5. Taxa displaying significant seasonal differences in numbers captured in net emergence traps. Values are mean nos. m^{-2} $night^{-1}$ (n = 12); means are back-transformed from log (c + 1); underlined means are significantly greater within taxon and substratum (ANOVA and S-N-K tests, $p < 0.05$). cop.: copepodites; =: means are equal

Taxon	Coral		Rubble		Grass		Mud	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Summer > Winter								
Pseudodiaptomus mertoni adults	=		=		1.7	0	=	
Pseudodiaptomus mertoni cop	=		=		1.6	0.2	=	
Ridgewayia spp.	9.2	0	4.6	0.1	=		=	
Oithona spp.	=		30.1	66.8	109.4	10.1	49.5	16.0
Miscellaneous cyclopoids	=		=		9.6	0.9	10.2	1.5
Parategastes sp.	11.7	5.6	=		53.7	125.4	20.4	6.7
Peltidium spp.	2.3	0.3	=		=		=	
Cumaceans	2.1	0.4	=		=		=	
Mysids	2.6	0.6	2.7	0.7	=		1.5	4.7
Tanaids	=		=		4.4	1.7	1.9	0.2
Miscellaneous nauplii	=		=		2.6	0	1.6	0.1
Zoeae	15.8	0	1.0	0.1	=		1.1	0
Megalopa	=		=		4.1	0.6	=	
Caridean/anomuran larvae	2.6	0.2	=		4.9	0.2	6.5	1.1
Sagitta spp.	1.7	0.2	=		1.8	0	2.3	0.1
Polychaetes	=		=		8.3	1.5	3.7	0.9
Gastropods	13.6	2.0	7.7	3.2	93.8	12.7	15.7	1.6
Gastropod veligers	61.9	28.4	=		62.2	32.7	=	
Winter > Summer								
Pseudodiaptomus colefaxi ♂♂	2.3	31.9	2.2	46.6	52.3	9.7	12.7	26.6
Pseudodiaptomus colefaxi ♀♀	1.3	7.0	0.4	7.4	6.2	0.5	=	
Pseudodiaptomus colefaxi ovigerous ♀♀	1.2	19.3	1.0	33.0	5.8	1.3	2.0	7.2
Pseudodiaptomus colefaxi cop.	2.0	19.0	1.1	19.0	=		=	
Stephos spp.	1.0	12.6	0.3	6.5	=		1.2	3.4
Acartia spp. adults	4.2	47.5	5.2	48.3	=		=	
Acartia spp. cop.	7.4	105.7	9.6	122.0	=		=	
Parvocalanus spp.	3.9	17.6	5.3	21.9	=		=	
Calanoid cop.	9.1	41.3	7.8	28.9	=		8.1	20.4
Miscellaneous harpacticoids	68.9	125.4	61.2	121.8	=		226.8	89.3
Copepod nauplii	67.1	374.3	38.6	313.5	=		103.1	237.7
Amphipods	=		=		10.4	54.6	3.0	15.4
Ostracods	4.1	8.9	3.1	14.6	=		=	
Cirripede larvae	1.3	39.6	1.1	14.7	7.1	0.9	1.2	3.6
Larvaceans	2.9	29.9	2.1	27.5	4.0	0.8	=	
Polychaete larvae	6.2	16.7	2.6	15.4	=		=	
Bivalve veligers	87.3	1163.7	123.5	1272.1	=		108.4	341.3
Summer = Winter								
Miscellaneous calanoids	2.6	8.2	4.0	9.2	17.6	0.8	10.2	1.7

exhibited significant effects. In 28 cases, a significant interaction was found among season, lunar period, substratum, and time of first emergence. Five groups had significant interaction effects at other levels, and a main effect due to time of first emergence was revealed for gastropod veligers. Of the 34 taxa with significant effects due to time of first emergence, 28 had peaks in emergence of greater than 10 zooplankters m^{-2} $90min^{-1}$. Temporal patterns in emergence in these 28 taxa were assigned to 5 categories (Table 10, Fig. 1). Sunset emergence (Fig. 1a, b), a sharp peak in numbers captured near twilight, was the most common pattern with 56 occurrences in 14 taxa. Nocturnal migration (Fig. 1c) with maximum emergence covering a broad part of the night or dissociated from sunset and sunrise appeared 18 times in 12 taxa. A sharp peak in emergence near sunrise was observed once for polychaetes (Fig. 1d). A bimodal pattern (Fig. 1e, f), 2 peaks in emergence within 1 night, was recorded on 9 occasions for 5 different groups. Nine taxa displayed a diurnal pattern (Fig. 1g, h), maximum emergence during the daytime, in 13 sets of samples. The 6 groups with peaks of emergence of less than 10 individuals m^{-2} $90min^{-1}$ were characterized by diurnal emergence in 3 cases – *Metis holothuriae*, tanaids, and tunicate larvae – and nocturnal emergence for carideans, isopods, and *Spadella cephaloptera*.

Emergence patterns in 9 taxa with statistically equal numbers emerging m^{-2} $90min^{-1}$ were classified by examination of the data. Harpacticoid copepods in the genus *Peltidium* exhibited sunset emergence (18:00 to 22:30 h, 46 % of the total number captured). Another harpacticoid, *Parategastes* sp., emerged mainly at night (18:00 to 01:30 h, 68 % of the total number), Diurnal emergence was exhibited by *Acartia* spp. copepodites, calanoids in the genus *Parvocalanus*, calanoid copepodites, miscellaneous cyclopoid copepods, cirripede larvae, miscellaneous nauplii, and gastropods (15:00 to 18:00 h and 04:30 to 12:00 h, between 31 and 71 % of the total number).

The presence of interaction effects in most ANOVAs performed on unpooled RET data meant each taxon exhibited significant temporal patterns in emergence only during certain sampling periods. The distribution

Table 6. Taxa displaying significant differences in numbers captured in net emergence traps among substrata. Values are mean nos. m^{-2} night $^{-1}$ (n = 12); means are back-transformed from log (c +1); underlined means are significantly greater within taxon and season (ANOVA and S-N-K tests, p < 0.05). cop.: copepodites; =. means are equal

Taxon	Summer				Winter			
	Coral	Rubble	Grass	Mud	Coral	Rubble	Grass	Mud
Coral >								
Zoeae	15 8	1 0	0.4	1.1			=	
Coral, Rubble >								
Pseudodiaptomus colefaxi cop.			=		19.0	19.0	1 6	4.2
Pseudodiaptomus mertoni adults	7 3	5.7	1.7	0 3	4.6	3.5	0	0 1
Stephos spp			=		12.6	6.5	3.1	3.4
Ridgewayia spp.	9.2	4.6	0.1	0.7			=	
Parvocalanus spp			=		17.6	21.9	6.6	7.6
Larvaceans			=		29.9	27.5	0.8	6 0
Polychaetes			=		6.6	4.0	1.5	0.9
Grass >								
Metis holothuriae	0.1	0	4.6	1.4	0 2	0 1	2.7	0.4
Parategastes sp	11.7	5.3	53.7	20.4	5 6	5 0	125.4	6.7
Peltidium spp.			=		0.3	0.9	2.8	0 4
Miscellaneous harpacticoids	68.9	61 2	792.0	226.8	125.4	121.8	570.3	89 3
Amphipods			=		8.7	9.3	54.5	15 4
Isopods	0.1	0.2	1.6	0.3			=	
Megalopa	0.5	0.9	4.1	0.5			=	
Gastropods	13.6	7 7	93.8	15.7	2.0	3.2	12.7	1.6
Grass, Mud >								
Miscellaneous cyclopoids	1.9	3.1	9.6	10.2			=	
Mysids			=		0.6	0.7	3.5	4.7
Ostracods	4.1	3.1	21.4	10.6			=	
Tanaids	0.1	0	4.4	1.9			=	
Polychaete larvae	6.2	2.6	17.9	14.0			=	
Coral, Grass >								
Cirripede larvae	1.3	1.1	7.1	1 2	39.6	14.7	0 9	3.6
At least 3 substrata =								
Pseudodiaptomus colefaxi ♂♂	2.3	2.2	52.3	12.7	31.9	46.6	9.7	26.6
Pseudodiaptomus colefaxi ♀♀	1.3	0.4	6.2	2.7	7.0	7.4	0.5	5.4
Pseudodiaptomus colefaxi ovigerous ♀♀	1 2	1.0	5.8	2.0	19.3	33.0	1.3	7.2
Acartia spp. adults	4 2	5.2	5.0	12.6	47.5	48.3	8 7	13.8
Acartia spp. cop	7 4	9.6	17.4	25.5	105.7	122.0	32 3	35.3
Miscellaneous calanoids	2.6	4.0	17.6	10.2	8.2	9.2	0.8	1.7
Calanoid cop.			=		41.3	28.9	9.9	20.4
Oithona spp	49.6	30.1	109.4	49.5	68.5	66.8	10 1	16.0
Cumaceans	2 1	2.3	2.0	0.3			=	
Bivalve veligers	87 3	123.5	258.4	108.4	1163.7	1272.1	236 9	341.3

of significant temporal patterns with peaks in emergence of more than 10 individuals was relatively even between seasons, among lunar periods, and among substrata (Table 11). Zooplankters emerged in sufficient numbers to generate statistically significant temporal patterns during all sampling periods. In addition, emergence peaks were observed during all phases of the tide (Fig. 1).

Ten taxa displayed more than one pattern in emergence (Table 10, Fig. 1). Typically, the patterns exhibited were sunset emergence, nocturnal emergence, and bimodal emergence. Variations in temporal patterns tended to be consistent for age and sex classes within the 2 species of *Pseudodiaptomus* (Table 10, Fig. 1a, b, e, f).

Multiple comparisons applied to unpooled RET data established or confirmed seasonal differences in emergence for various taxa. *Pseudocyclops* spp., miscellaneous calanoid copepods, *Metis holothuriae*, miscellaneous harpacticoids, carideans, isopods, ostracods, tanaids, miscellaneous nauplii, *Spadella cephaloptera*, larvaceans, polychaetes, polychaete larvae, bivalve veligers, and tunicate larvae were shown to have emerged in greater numbers in the summer. *Acartia* spp. copepodites, calanoid copepodites, miscellaneous cyclopoid copepods, *Paraetegastes* sp., and copepod nauplii were more numerous in winter samples. All 4 groups of *Pseudodiaptomus colefaxi*, as well as cirripede larvae, emerged in nearly equal numbers during both seasons.

Variations in emergence among lunar periods were indicated by some ANOVAs. *Pseudodiaptomus colefaxi* females and copepodites, *Acartia* spp. adults, *Peltidium* spp., miscellaneous harpacticoids, and mysids emerged in greater numbers during either lunar quarter or the new moon. Statistically significant emergence during the full moon was revealed for *P. colefaxi* males and ovigerous females, *Oithona* spp., and chaetognaths in the genus *Sagitta*. Equal emergence in all 4 lunar periods was indicated for *Parvocalanus* sp., calanoid copepodites, amphipods, cumaceans, and gastropods.

Analysis of unpooled RET data clarified substratum-

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Table 7. Taxa displaying significant seasonal differences in numbers captured in RETs. Values are mean nos. m^{-2} night $^{-1}$ ($n = 2$); means are back-transformed from log ($c + 1$); underlined means are significantly greater within taxon, lunar period, and substratum (ANOVA and S-N-K tests, $p < 0.05$). FQ: first quarter; FM: full moon; LQ: last quarter; NM: new moon; cop.: copepodites; =: means are equal

Taxon/substratum	FQ		FM		LQ		NM	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Summer > Winter								
Pseudodiaptomus colefaxi ♂♂								
Coral	=		=		25.0	7 8	=	
Grass	55.4	289.1	278.2	38.0	311.1	55.9	175.4	53.5
Mud	11.7	151.4	=		304.2	31.8	=	
Pseudodiaptomus mertoni ♂♂								
Coral	238.9	1.8	73.1	2.5	101.3	1.4	=	
Grass	99.0	0.4	29.2	0.7	34.5	0	13.8	1.0
Mud	11.9	0	7.3	0.4	11.6	0.7	4.2	1.0
Pseudodiaptomus mertoni ♀♀								
Coral	140.2	1.0	48.0	2.9	57.9	1.0	40.7	6 4
Grass	96.7	1.4	39.7	0	32.1	0	30.6	0
Mud	16.8	0.4	5.3	0.4	9.5	0	=	
Pseudodiaptomus mertoni cop.								
Coral	554.0	0.4	197.1	1.0	253.3	0.4	147.1	10.6
Grass	84.1	1.4	123.7	0.4	196.1	0	106.2	1.0
Mud	51.7	1 6	47.0	0.4	102.4	0	37.8	0
Ridgewayia spp.								
Coral	14.6	2.2	53.7	0 4	40.6	0.4	18.0	0.4
Grass	=		9.5	0 4	12.3	1.4	10.4	0.7
Mud	=		4.7	0	9.2	0	1.8	0
Miscellaneous calanoids								
Coral	428.4	86.0	99.4	11.0	629.3	5.7	=	
Grass	154.9	44 9	168.2	4.9	504.0	7 4	72.5	6.4
Mud	=		104.4	8.9	282.0	4.9	36.8	5.7
Oithona spp.								
Coral	3240.4	830.5	2830.4	667.5	2476.0	491.3	=	
Grass	3640.7	884.9	3288.1	446.6	3058.3	552.3	1839.0	392.9
Mud	3216.8	843.1	3749.3	591.2	2315.7	359.9	1676.2	441.7
Metis holothuriae								
Coral	=		=		=		6.3	0
Grass	24.1	92.2	30.7	8.9	=		49.1	10.7
Mud	2.7	11.5	35.9	8 9	=		44.7	3.2
Peltidium spp.								
Coral	16.0	2.9	7.5	0 7	=		36.0	2 0
Grass	10.0	47.4	15.6	4.9	=		41.0	3 0
Mud	2.2	7.8	10.5	0.7	=		9.2	2.2
Miscellaneous harpacticoids								
Coral	3177.8	744.8	2788.9	897.2	3670.0	785.1	=	
Mud	=		=		2655.8	395.3	=	
Carideans								
Coral	8.8	0.4	=		5.0	0	=	
Grass	29.6	1.0	8.8	0	8.7	1.2	3.0	0
Mud	=		2.5	0	12.1	2.9	=	
Cumaceans								
Coral	=		46.7	7 4	43.5	7 4	23.9	4.3
Grass	=		89.5	6 3	=		=	
Mud	0	13.1	=		=		=	
Isopods								
Coral	=		=		=		4.8	0
Grass	2.7	0.4	5.3	0.4	=		=	
Mud	=		=		=		7.4	0
Mysids								
Coral	14.5	3.2	62.1	7.5	65.1	6 5	82.9	5.0
Grass	42.9	28.8	56.2	5.5	=		=	
Ostracods								
Coral	=		33.5	10.6	87.3	15.5	118.9	1.8
Grass	446.9	14.5	92.4	3.9	185.3	7.9	370.1	3.6
Mud	116.7	10.5	69.0	4.5	291.4	2.0	279.1	4.5
Zoeae								
Coral	137.2	6.5	53.3	3.9	22.7	5.0	77.9	5.3
Grass	19.0	2.5	11.6	39.2	49.4	15.2	59.5	14.2
Mud	14.7	3.0	=		26.0	4.0	=	
Megalopa								
Coral	=		=		=		2.0	0
Grass	=		200.5	2.0	5.9	1.0	7.8	1.4
Mud	0.4	7.8	=		=		4.5	16.7
Caridean/anomuran larvae								
Coral	19.5	0	27.6	0	132.7	0	43.1	0
Grass	24.1	0.7	80.6	8.8	93.1	0	80.0	1.4
Mud	9.2	1.8	92.7	13.9	51.3	1 0	50.6	1.0

Table 7 (continued)

Taxon/substratum	FQ		FM		LQ		NM	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Summer > Winter								
Spadella cephaloptera								
Coral	14.6	0.4	=		=		17.4	1.0
Grass	4.5	0.4	14.3	0.4	=		25.5	0
Mud	4.7	0	=		=		30.5	0
Sagitta spp.								
Coral	184.4	1.8	70.2	1.8	397.7	1.8	=	
Grass	212.5	6.0	399.7	0.4	235.5	0.4	51.0	1.4
Mud	309.3	2.5	255.8	1.4	267.1	0.7	29.5	0.4
Larvaceans								
Coral	=		761.0	43.5	1126.1	23.7	181.3	10 350.4
Grass	46.2	11.7	316.9	72.4	1094.7	3.6	187.5	2166.5
Mud	88.5	15.6	364.0	77.9	871.1	5.6	34.0	1448.6
Polychaete larvae								
Coral	287.0	85.5	=		=		=	
Grass	=		=		328.9	85.3	=	
Mud	=		=		377.8	101.3	=	
Gastropods								
Coral	487.9	0.7	349.2	0	123.5	0.4	225.1	0.4
Grass	741.8	8.4	740.9	17.4	385.5	5.3	571.7	12.4
Mud	207.4	2.9	199.0	14.3	272.9	0	86.4	6.5
Bivalve veligers								
Coral	3833.3	7.0	5191.4	137.4	1550.4	217.9	1086.6	4752.9
Grass	1210.3	16.9	1609.1	133.9	4349.4	128.4	=	
Mud	377.4	0.4	772.1	128.1	1293.1	64.5	435.8	1247.2
Tunicate larvae								
Coral	=		=		=		3.0	0.4
Grass	=		=		=		3.6	0
Mud	=		7.4	0.4	23.5	3.2	3.9	0.4
Winter > Summer								
Acartia spp. adults								
Coral	=		14.9	244.4	1378.7	106.2	40.8	17 040.9
Grass	348.9	65.4	=		=		87.4	467.7
Mud	112.9	363.3	=		=		32.2	532.0
Stephos spp.								
Coral	1.8	39.7	3.0	39.4	2.2	44.5	3.5	15.5
Grass	11.8	36.1	=		=		=	
Mud	2.2	7.5	=		=		=	
Parvocalanus sp.								
Coral	341.5	1053.4	199.2	525.7	=		182.2	1031.7
Mud	=		=		547.8	86.7	120.6	499.8
Miscellaneous cyclopoids								
Coral	=		63.7	318.5	=		98.5	525.1
Grass	=		52.7	248.0	=		=	
Mud	=		35.1	235.5	=		49.6	332.6
Paralegastes sp.								
Coral	=		=		85.8	320.1	=	
Grass	657.6	10 207.2	651.9	1724.9	412.4	21512.7	=	
Mud	56.3	243.5	=		32.0	103.6	=	
Summer = Winter								
Amphipods								
Coral	27.6	87.4	=		=		=	
Grass	70.4	379.9	=		=		=	
Mud	4.9	104.5	=		=		28.2	80.7
Gastropod veligers								
Coral	=		87.5	550.1	=		299.9	1485.9
Grass	=		87.3	690.5	806.0	208.7	=	
Mud	=		106.3	375.9	=		=	
Pseudodiaptomus colefaxi ♀♀								
Grass	14.5	60.9	82.2	7.1	84.0	20.3	=	
Mud	2.9	36.8	=		84.0	20.3	24.4	67.5
Pseudodiaptomus colefaxi ovigerous ♀♀								
Grass	16.3	103.1	110.6	5.5	127.7	24.1	59.5	16.0
Mud	6.7	40.8	=		125.4	9.1	1.8	13.5

Table 7 (continued)

Taxon/substratum	FQ			FM			LQ			NM		
	Summer		Winter	Summer		Winter	Summer		Winter	Summer		Winter
Summer = Winter												
Pseudodiaptomus colefaxi cop												
Coral		=			=		93.8		7 8		=	
Grass	14 2		129.2	60.9		16.7		=			=	
Mud	5.9		125.4		=		157.4		20 8		=	
Acartia spp. cop.												
Coral		=			=		2081.3		408.1	269 6		16 448.9
Grass	646.1		282.5		=			=			=	
Mud	453.4		758.4		=		851.4		306.9	240.0		1541.2
Pseudocyclops spp.												
Coral		=		32.0		5.9		=			=	
Grass	3.9		19.5		=		3.0		10.5		=	
Calanoid cop												
Coral		=			=			=		502.3		4190.1
Mud		=			=		1178.6		289.9	242 9		1279.4
Copepod nauplii												
Coral		=			=			=		1779 2		6286.2
Mud		=			=		10 240.3		1012 9		=	
Tanaids												
Coral		=		3.0		0.4		=			=	
Grass		=		35.7		9.6		=			=	
Mud	1 4		5.9		=			=			=	
Miscellaneous nauplii												
Coral	27.0		350.8		=			=	8.9		=	5.9
Grass	20.0		157.8	73.9		24.5	92.3		12.0	26.5		
Mud	5.0		203.1		=		84.6				=	
Cirripede larvae												
Coral		=			=		943.8		110.5	107.5		329.3
Grass		=			=		589.2		79.0		=	
Mud	6.0		35.9		=		438.8		69 7		=	
Polychaetes												
Coral	22.4		277.0	23.9		5 0		=			=	
Mud	8.9		29 2		=			=			=	

related emergence patterns for 34 taxa. All 3 groups of *Pseudodiaptomus colefaxi* adults, *Stephos* spp., carideans, mysids, ostracods, tanaids, caridean/anomuran larvae, zoeae, and *Sagitta* spp. were shown to have emerged in greater numbers from grass. *Pseudodiaptomus mertoni* males, females, and copepodites, *Acartia* spp. adults and copepodites, *Pseudocyclops* spp., *Ridgewayia* sp., *Parvocalanus* sp., miscellaneous calanoid copepods, calanoid copepodites, cirripede larvae, miscellaneous nauplii, larvaceans, polychaetes, polychaete larvae, gastropod veligers, and bivalve veligers were more numerous in samples taken above coral patches. *Oithona* spp., miscellaneous cyclopoid copepods, cumaceans, and *Spadella cephaloptera* were equally common in samples from coral and grass. Copepod nauplii and tunicate larvae were taken in equal numbers from all substrata.

DISCUSSION

Differences in sampling methodology and taxonomic classification have led to dispute over the importance of demersal zooplankton in various ecosystems (Alldredge & King 1977, 1985, Porter et al. 1977, Hobson & Chess 1979, Robichaux et al. 1981, Youngbluth 1982a). A definition of demersal zooplankton relies on an understanding of the animals' behavior, particularly in relation to the substratum. Emergence traps and re-entry traps have been the primary tools used to sample demersal zooplankton. Both methods have biases including incidental trapping of non-demersal forms during deployment or recovery, capture of animals that crawl into traps, and contamination of emergence samples by zooplankters forced into traps through gaps between the bases and the bottom. In this study and a previous one (Jacoby & Greenwood 1988), samples from net tows, re-entry traps, and emergence traps were compared in order to obtain a better idea of the distribution and behavior of various zooplankters.

Sixteen of the 43 common taxa in this study consisted of adults which were captured predominantly in re-entry or emergence traps. These taxa displayed night-time emergence and were rare in net tows or were clearly more common in night-time net tows. These groups (i.e. *Pseudodiaptomus colefaxi* males, females, and ovigerous females, *Stephos* spp., *Pseudocyclops* spp., *Ridgewayia* sp., *Parategastes* sp., *Peltidium* spp., amphipods, carideans, cumaceans, isopods, mysids, ostracods, *Spadella cephaloptera*, and polychaetes) were classified as demersal zooplankters. They were on or near the bottom during the day and emerged at night, although they may not have reached the surface of the water column in large numbers. This assemblage includes the largest zooplankters commonly captured.

Two other taxa, *Pseudodiaptomus mertoni* males and

Table 8. Taxa displaying significant differences in numbers captured in RETs among lunar periods. Values are mean nos. m^{-2} night $^{-1}$ (n = 2); means are back-transformed from log (c + 1); underlined means are significantly greater within taxon, season, and substratum (ANOVA and S-N-K tests, $p < 0.05$). FQ: first quarter; FM: full moon; LQ: last quarter; NM: new moon; cop.: copepodites; =: means are equal

Taxon/substratum	Summer				Winter			
	FQ	FM	LQ	NM	FQ	FM	LQ	NM
LQ, NM >								
Pseudodiaptomus mertoni cop								
Coral		=			0.4	1.0	0.4	$\underline{10.6}$
Stephos spp.								
Mud	2.2	3.5	7.5	$\underline{26.5}$		=		
Acartia spp. cop								
Coral	643.6	328.4	$\underline{2081.3}$	269.6	335 5	371 2	408.1	$\underline{16448.9}$
Copepod nauplii								
Mud	1373.9	3117.6	$\underline{10240.3}$	2055.0		=		
Isopods								
Coral	0.7	0 4	0	$\underline{4.8}$		=		
Mud	0.4	1.2	1.0	$\underline{7.4}$		=		
Bivalve veligers								
Coral		=			7.0	137.4	217.9	$\underline{4752.9}$
Grass	1210.3	1609 1	$\underline{4349.4}$	863.7	16.9	133.9	128.4	$\underline{935.6}$
Mud		=			0.4	128.1	64.5	$\underline{1247.2}$
FQ, LQ, NM >								
Pseudodiaptomus mertoni ♂♂								
Coral		=			1.8	2.5	1 4	$\underline{19.9}$
Grass	$\underline{99.0}$	29.2	34.5	13 8		=		
Mud		=				=		
Pseudodiaptomus mertoni ♀♀								
Coral		=				=		
Grass		=				=		
Mud		=			0.4	0.4	0	$\underline{3.5}$
Miscellaneous calanoids								
Coral	$\underline{428.4}$	99 4	$\underline{629.3}$	81.0	$\underline{86.0}$	11.0	5 7	$\underline{97.6}$
Grass	154.9	168 2	$\underline{504.0}$	72.5	$\underline{44.9}$	4.9	7 4	6.4
Mud	$\underline{174.2}$	$\underline{104.4}$	$\underline{282.0}$	36.8	$\underline{154.8}$	8.9	4 9	5.7
Parategastes sp.								
Grass		=			$\underline{10207.2}$	1724 9	2152 7	960.2
Mud	56.3	131 7	32.0	$\underline{351.5}$		=		
Carideans								
Grass	$\underline{29.6}$	8.8	8.7	3.0		=		
Mud		=			$\underline{3.9}$	0	$\underline{2.9}$	$\underline{3.5}$
Ostracods								
Coral		=			$\underline{46.4}$	10 6	15.5	1.8
Miscellaneous nauplii								
Coral		=			$\underline{350.8}$	14.2	24.1	54.0
Grass	20.0	$\underline{73.9}$	$\underline{92.3}$	26.5	$\underline{157.8}$	24.5	8.9	5 9
Mud	5.0	25.5	$\underline{84.6}$	25.1	$\underline{203.1}$	26.3	12.0	38 7
Spadella cephaloptera								
Coral	$\underline{14.6}$	1.0	2.2	$\underline{17.4}$		=		
Grass	4.5	14 3	0	$\underline{25.5}$		=		
Mud	4.7	1.4	0.4	$\underline{30.5}$		=		
Polychaetes								
Coral	22.4	23.9	$\underline{172.2}$	35.0	$\underline{277.0}$	5.0	$\underline{189.2}$	16.0
Grass		=			$\underline{90.0}$	23.5	$\underline{92.2}$	14.8
FM + Others >								
Pseudocyclops spp.								
Grass	3.9	$\underline{15.1}$	3.0	2.9		=		
Ridgewayia spp								
Grass	2.5	$\underline{9.5}$	$\underline{12.3}$	$\underline{10.4}$		=		
Mud	0	$\underline{4.7}$	$\underline{9.2}$	$\underline{1.8}$		=		
Parvocalanus sp.								
Mud		=			$\underline{351.5}$	$\underline{647.1}$	86.7	$\underline{499.8}$
Calanoid cop.								
Coral		=			1496.9	795.3	1010.2	$\underline{4190.1}$
Mud		=			$\underline{1121.1}$	$\underline{817.5}$	289.9	$\underline{1279.4}$
Metis holothuriae								
Coral	$\underline{5.0}$	0.4	0.7	$\underline{6.3}$		=		
Grass		=			$\underline{92.2}$	8.9	22.0	10.7
Mud	2.7	$\underline{35.9}$	7 9	$\underline{44.7}$		=		
Miscellaneous cyclopoids								
Mud		=			22.8	$\underline{235.5}$	72.9	$\underline{332.6}$
Tanaids								
Mud	1.4	$\underline{16.3}$	2.5	$\underline{11.8}$		=		
Zoeae								
Grass		=			2.5	$\underline{39.2}$	$\underline{15.2}$	$\underline{14.2}$
Mud		=			3.0	$\underline{18.2}$	4.0	$\underline{46.3}$
Megalopa								
Grass	7.4	$\underline{200.5}$	5.9	7.8	$\underline{9.2}$	2.0	1.0	1.4

Table 8 (continued)

Taxon/substratum	Summer FQ	Summer FM	Summer LQ	Summer NM	Winter FQ	Winter FM	Winter LQ	Winter NM
FM + Others >								
Caridean/anomuran larvae								
Coral	19.5	27.6	132.7	43.1		=		
Grass	24.1	80.6	93.1	80.0	0.7	8.8	0	1.4
Mud	9.2	92.7	51.3	50.6	1 8	13.9	1.0	1.0
Cirripede larvae								
Coral	27.9	62.9	943.8	107.5		=		
Grass	21 2	156.0	589.2	59.8	37.5	246.5	79.0	72.8
Mud	6 0	83.3	438.8	27.7	35.9	212.7	69 7	52.9
Larvaceans								
Coral	34.3	761.0	1126.1	181 3	70.3	43.5	23.7	10350.4
Grass	46.2	316.9	1094.7	187 5	11.7	72.4	3.6	2166.5
Mud	88.5	364.0	871.1	34.0	15.6	77.9	5.6	1448.6
Polychaete larvae								
Grass		=			32.4	318.2	85.3	205.8
Gastropod veligers								
Coral		=			81.0	550.1	424.3	1485.9
Grass	92.4	87.3	806.0	169.2	38.5	690.5	208.7	214.1
Mud	34.0	106.3	272.4	147.8	51.5	375.9	106.9	371.6
Tunicate larvae								
Coral	1.4	17.4	5.9	3.0	1.6	7.0	8.8	0.4
Grass	1.8	2.0	13.1	3.6	2.0	4.5	10.5	0
Mud	1.2	7 4	23.5	3.9	4.7	0.4	3.2	0.4
Lunar periods =								
Pseudodiaptomus colefaxi ♂♂								
Coral		=			36.8	80.1	7.8	54.5
Grass	55 4	278.2	311.1	175.4	289.1	30.8	55.9	53.5
Mud	11.7	148.7	304.2	21.0		=		
Pseudodiaptomus colefaxi ♀♀								
Grass	14.5	82.2	84.0	100.0	60.9	7 1	20.3	41.8
Mud	2 9	46.4	84.0	24.4		=		
Pseudodiaptomus colefaxi ovigerous ♀♀								
Coral		=			7.9	33 2	6.5	25.6
Grass	16.3	110.6	127.7	59.5	103.1	5 5	24.0	16.0
Mud	6.7	54.0	125.4	1.8		=		
Pseudodiaptomus colefaxi cop.								
Coral		=			109.7	40.6	7 8	26.0
Gras	14.2	60.9	101.5	78.7		=		
Mud	5.9	34.7	157.4	29.4		=		
Acartia spp. adults								
Coral	246.0	14.9	1378.7	40.8	358.7	244.4	106.2	17040.9
Mud	112.9	188.9	229.5	32.2		=		
Peltidium spp.								
Grass		=			47.4	4.9	20.9	3.0
Mud	2.2	10.5	1.4	9.2	7.8	0.7	0.4	2.2
Amphipods								
Grass		=			379.9	79.4	119.9	105 5
Mud	4.9	40.8	39.1	28.2		=		
Cumaceans								
Grass	68.1	89.5	20.0	10.8	90.7	6 3	11.8	16 1
Mud	0	4.0	3.2	6.9		=		
Mysids								
Coral	14.5	62.1	65.1	82.9		=		
Grass		=			28.8	5 5	29 2	29.4
Mud	3.5	10.6	13.8	35.1		=		
Sagitta spp								
Coral	184.4	70.2	397.7	18.4	1.8	1.8	1.8	11.0
Grass	212.5	399.7	235.5	51.0	6.0	0.4	0 4	1.4
Mud	309.3	255.8	267.1	29.5		=		

females, were rare in re-entry traps, emerged at night, and were equally common in daytime and night-time net tows. This calanoid appears to have been distributed throughout the water column during the day with an increase in numbers near the surface at night. Perhaps this species should be considered a demersal zooplankter loosely associated with the substratum.

Six taxa comprised of small or transparent adults did not exhibit behavior typical of demersal zooplankton. These groups were rare in re-entry trap samples, were common in emergence trap samples, were taken in nearly equal numbers in daytime and night-time net tows, and displayed diurnal emergence. Due to their behavior, these 6 taxa (*Acartia* spp. adults *Parvocalanus* sp., miscellaneous calanoids, miscellaneous cyclopoids, *Metis holothuriae*, and *Sagitta* spp.) could be considered holoplanktonic contaminants of emergence traps that were accidently captured during trap deployment or entered through gaps at the bases of the traps (Robichaux et al. 1981).

In this study, cod ends were not attached to emergence traps until they were on the bottom; therefore, few individuals would have been trapped above 70 cm into the water column. Weighted skirts eliminated gaps at the bases of net traps, and RETs sealed well on the grass substratum. Gaps at the bases of the RETs were less than 4 cm on coral and mud bottoms, therefore zooplankters swept into any gaps must have been within a few centimeters of the bottom.

The capture of reasonable numbers of these 6 taxa by RETs and net emergence traps from all types of bottom was not regarded as only incidental. Populations of these taxa appear to have been distributed throughout the water column during the day, including near the bottom. Daytime distributional maxima near the bottom in shallow water have been reported for some of these taxa (Oug 1977, Stearns 1986, Ueda 1987, Jacoby & Greenwood 1988). These taxa did not fit a strict definition of demersal zooplankton because they were found in the water column during the day and they showed daytime emergence. However, their presence near the bottom may be important to future studies of zooplankton in shallow water ecosystems.

Oithona spp., miscellaneous harpacticoids, tanaids, larvaceans, and gastropods were most common in re-entry traps or night tows but they exhibited diurnal emergence patterns. Gastropods obviously did not swim into re-entry or emergence traps and were considered to be contaminants due to crawling. Tanaids fit the pattern expected for demersal zooplankton except they emerged primarily into the first sampling bottle (15:00 to 16:30 h). Only low numbers emerged, and movement may have been a result of disturbance during trap deployment. Therefore, tanaids were regarded as demersal animals that did not emerge in large numbers. Miscellaneous harpacticoids typically emerged in equal numbers throughout the 21 h sampling period except for one instance of peak emer-

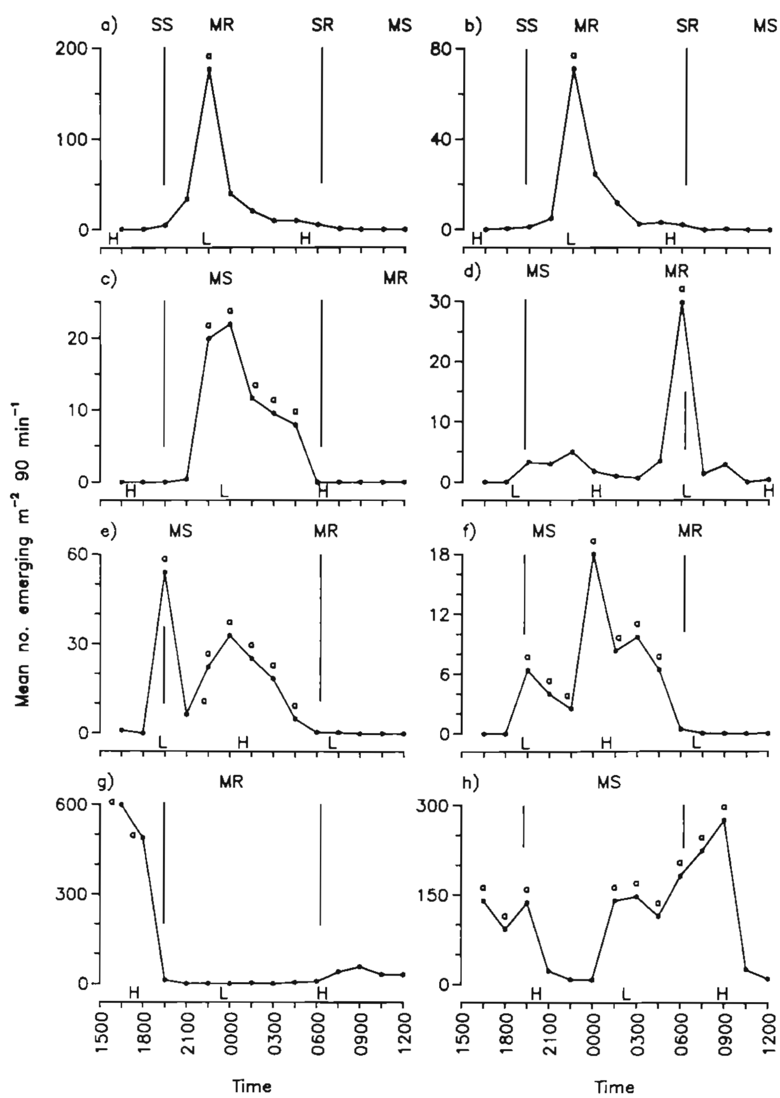

Fig. 1. Mean number of zooplankters emerging m^{-2} 90min^{-1} ($n = 2$). (a) *Pseudodiaptomus colefaxi* males from summer, last quarter, mud; (b) *P. colefaxi* ovigerous females from summer, last quarter, mud; (c) *P. colefaxi* males from summer, first quarter, coral; (d) polychaetes from summer, new moon, coral; (e) *P. colefaxi* males from summer, new moon, grass; (f) *P. colefaxi* ovigerous females from summer, new moon, grass; (g) *Acartia* spp. adults from summer, last quarter, coral; (h) miscellaneous harpacticoids from summer, first quarter, mud. SS, SR, and vertical rules: sunset and sunrise; MR: moonrise; MS: moonset; H: high tide; L: low tide. a: mean is significantly greater than unlabeled means as shown by ANOVA and S-N-K tests ($p > 0.05$)

Table 9. Taxa displaying significant differences in numbers captured in RETs among substrata. Values are mean nos. m^{-2} night $^{-1}$ (n = 2); means are back-transformed from log (c + 1); underlined means are significantly greater within taxon, season, and lunar period (ANOVA and S-N-K tests, $p < 0.05$). FQ: first quarter; FM: full moon; LQ: last quarter; NM: new moon; cop.. copepodites; =: means are equal

Taxon/lunar period	Summer			Winter		
	Coral	Grass	Mud	Coral	Grass	Mud
Coral >						
Pseudodiaptomus colefaxi cop.						
FQ	60.3	14.2	5.9		=	
Ridgewayia spp.						
FQ	14.6	2.5	0		=	
FM	53.7	9.5	4.7		=	
LQ	40.6	12.3	9.2		=	
NM	18.0	10.4	1.8		=	
Miscellaneous calanoids						
NM		=		97.6	6.4	5.7
Calanoid cop						
NM		=		4190.1	743.7	1279.4
Oithona sp.						
NM		=		1893.4	392.9	441.7
Larvaceans						
FQ		=		70.3	11.7	15.6
LQ		=		23.7	3.6	5.6
NM	181.3	187.5	34.0	10350.4	2166.5	1448.6
Polychaete larvae						
FQ	287.0	58.0	42.5		=	
Coral, Grass >						
Pseudodiaptomus mertoni ♂♂						
FQ	238.9	99.0	11.9		=	
FM	73.1	29.2	7.3		=	
LQ	101.3	34.5	11.6		=	
NM	32.1	13.8	4.2	19.9	1.0	1.0
Pseudodiaptomus mertoni ♀♀						
FQ	140.2	96.7	16.8			
FM		=		2.9	0	0.4
LQ	57.9	32.1	9.5		=	
NM	40.7	30.6	3.6	6.4	0	3.5
Pseudodiaptomus mertoni cop.						
FQ	554.0	84.1	51.7		=	
FM	197.1	123.7	47.0		=	
NM	147.1	106.2	37.8	10.6	1.0	0
Pseudocyclops spp.						
FQ	5.0	3.9	0.7	7.8	19.5	0.4
FM	32.0	15.4	2.0	5.9	6.7	1.4
LQ	16.0	3.0	3.0	15.9	10.5	0.7
NM	13.0	2.9	2.2	15.3	4.9	2.2
Parvocalanus sp.						
FQ		=		1053.4	297.8	351.5
LQ		=		332.3	286.1	86.7
Miscellaneous cyclopoids						
FQ		=		103.9	107.3	22.8
LQ		=		223.7	224.0	72.9
Amphipods						
FQ	27.6	70.4	4.9	87.4	379.9	104.5
Cumaceans						
FQ	11.6	68.1	0	12.0	90.7	13.1
FM	46.7	89.5	4.0		=	
LQ	43.5	20.0	3.2		=	
Ostracods						
FQ	60.4	446.9	116.7	46.4	14.5	10.5
LQ		=		15.5	7.9	2.0
Cirripede larvae						
FQ	27.9	21.2	6.0		=	
NM		=		329.3	72.8	52.9
Gastropods veligers						
FQ	121.4	92.4	34.0		=	
NM		=		1485.9	214.1	371.6
Bivalve veligers						
FQ	3833.3	1210.3	377.4	7.0	16.9	0.4
FM	5291.4	1609.1	772.1		=	
LQ	1550.4	4349.4	1293.1		=	
NM		=		4752.9	935.6	1247.2
Grass >						
Parategastes sp.						
FQ	199.9	657.6	56.3	130.3	10207.2	243.5
FM	102.6	651.9	131.7	178.6	1724.9	335.9
LQ	85.8	412.4	32.0	320.1	2152.7	103.6
NM		=		167.1	960.2	568.7

Table 9 (continued)

Taxon/lunar period	Summer			Winter		
	Coral	Grass	Mud	Coral	Grass	Mud
Grass >						
Peltidium sp.						
FQ		=		2.9	47.4	7.8
FM		=		0.7	4.9	0.7
LQ	2.9	10.5	1.4	1.0	20.9	0.4
Miscellaneous harpacticoids						
FQ		=		744.8	6741.0	918.7
LQ		=		785 1	2433.4	395.3
Isopods						
FM	0.4	5.3	1 2		=	
Spadella cephaloptera						
FM	1 0	14.3	1.4		=	
Grass, Mud >						
Pseudodiaptomus colefaxi ♂♂						
FQ	78 4	55.4	11 7	36 8	289.1	151.4
LQ	25.0	311.1	304.2	7.8	55.9	31.8
NM	46.0	175.4	21 0		=	
Pseudodiaptomus colefaxi ovigerous ♀♀						
FQ		=		7.9	103 1	40.8
FM	15 4	110.6	54.0	33.2	5.5	26.5
LQ	8.5	127.7	125.4		=	
NM	15.3	59.5	1.8		=	
Metis holothuriae						
FQ	5.0	24.1	2.7	4 7	92 2	11.5
FM	0.4	30.7	35.9	0 7	8.9	8.9
LQ	0.7	12.5	7.9	2.0	22.0	4.5
NM	6.3	49.1	44.7	0	10.7	3.2
Carideans						
FQ	8.8	29.6	5.9		=	
FM	1.0	8.8	2.5		=	
NM		=		0.4	0	3.5
Caridean/anomuran larvae						
FM	27 6	80.6	92.7	0	8.8	13.9
Tanaids						
FQ	5 5	41.0	1.4	3 0	19.8	5.9
FM	3 0	35.7	16.3	0 4	9.6	8.8
LQ	1 8	16.1	2.5		=	
NM	0 4	18.0	11.8	1.0	18.5	15.0
Megalopa						
FQ	0.4	7.4	0 4	0	9.2	7.8
FM	0.4	200.5	1.0		=	
LQ	1.0	5.9	1 4		=	
NM		=		0	1.4	16.7
Gastropods						
FM		=		0	17.4	14.3
LQ		=		0 4	5.3	0
NM		=		0 4	12.4	6.5
Coral, Mud >						
Acartia spp. adults						
FQ		=		358.7	65.4	363.3
FM	14.9	69 8	188.9	244.4	73.2	238.5
LQ	1378.7	221.7	229.5			
NM		=		17 040.9	407.7	532 0
Acartia spp. cop.						
FQ		=		335.5	241 1	1265.4
NM		=		16 448.9	801 4	1541.2
Substrata =						
Pseudodiaptomus colefaxi ♀♀						
FQ	24.7	14.5	2.9		=	
FM		=		38.5	7.1	28.0
LQ	17.0	84.0	84.0		=	
NM	27 5	100.0	24.4		=	
Stephos spp.						
FQ	1.8	11.8	2.2	39.7	36.1	7.5
FM	3.0	30.3	3.5	39.4	28.8	8.9
LQ	2 2	9.9	7 5		=	
NM	3.5	28.0	26.5		=	
Mysids						
FQ	14.5	42.9	3.5	3.2	28.8	10.0
FM	62.1	56.2	10.6		=	
LQ	65.1	38.6	13.8	6.5	29.2	26.5
NM		=		5.0	29.4	44.0
Zoeae						
FQ	137.2	19.0	14.7		=	
FM	53.3	111.6	14 0	3.9	39.2	18.2
LM		=		5.0	15.2	4.0
NM		=		5.3	14.2	46.3

Table 9 (continued)

Taxon/lunar period	Summer Coral	Summer Grass	Summer Mud	Winter Coral	Winter Grass	Winter Mud
Substrata =						
Miscellaneous nauplii						
FQ	27.0	20.0	5.0			
NM	115.9	26.5	25.1	54.0	5.9	38.7
Sagitta spp.						
FM	70.2	399.7	255.8		=	
NM		=		11.0	1.4	0.4
Polychaetes						
FQ		=		277.0	90.0	29.2
FM		=		5.0	23.5	18.7
LQ	172.2	55.3	11.4	189.2	92.2	7.9
Tunicate larvae						
FM	17.4	2.00	7.4	7.0	4.5	0.4

gence during the day. This multispecific group probably contained some demersal taxa, as well as other holoplanktonic species (Walters & Bell 1986). *Oithona* spp. and larvaceans were taken in greater numbers in night-time net tows yet they displayed diurnal emergence patterns. Larvaceans were captured largely in the first sampling bottle and their emergence may have been caused by disturbance during trap deployment. *Oithona* spp. were taken in equal numbers in re-entry and emergence traps suggesting that some members of this genus were very close to the bottom during the day and could be classified as demersal zooplankters. Although *Oithona* spp. and larvaceans typically are considered holoplankters, their daytime distribution in shallow water appears to extend very near the bottom because they have been taken in emergence traps at several locations (Porter et al. 1977, Feeley et al. 1979, Ohlhorst 1982, Jacoby & Greenwood 1988).

Fourteen taxa in this study consisted of larval forms. Results indicated that only zoeae in the winter were more common near the surface during the day. *Pseudodiaptomus colefaxi* and *Pseudodiaptomus mertoni* copepodites, caridean/anomuran larvae, zoeae, megalopa, and bivalve veligers emerged predominantly at night. These taxa appeared to be near the bottom during the day. Gastropod veligers, which were more numerous in night tows, also may have belonged in this category if their statistically significant emergence into the first sampling bottle was due to disturbance. Later instars of *Pseudodiaptomus* spp. copepodites apparently exhibited a demersal habit similar to the adults of these species. Caridean/anomuran larvae, zoeae, and megalopa were large relative to most larvae, and they tended to be near the bottom during the day which could have reduced their availability to visual predators. In contrast, smaller or transparent larval forms which may have been less subject to visual predation, i.e. *Acartia* spp. copepodites, calanoid copepodites, cirripede larvae, and polychaete larvae, were common in daytime net tows and showed diurnal emergence or no pattern in emergence. Copepod nauplii, miscellaneous nauplii, and tunicate larvae probably should have been included in this assemblage because they exhibited diurnal emergence, but they were too small to be taken in net tows.

The taxa captured in emergence and re-entry traps in this study were similar to those previously for coral reefs (Alldredge & King 1977, Porter et al. 1977, Randall et al. 1978, Feeley et al. 1979, Hobson & Chess 1979, Birkeland & Smalley 1981, McWilliam et al. 1981, Walter et al. 1981, Ohlhorst 1982, Jacoby & Greenwood 1988), for subtidal sand flats (Alldredge & King 1980, 1985, Youngbluth 1982a, Stretch 1985), for seagrass beds (Robichaux et al. 1981, Alldredge 1985, Bell et al. 1986, Hicks 1986, Walters & Bell 1986), for kelp beds (Hammer & Zimmerman 1979, Hammer 1981), and for a temperate estuary (Thomas & Jelley 1972). Comparisons of numbers of zooplankters captured were hampered by differences in classification and methodology, but the total numbers of zooplankters captured in this study (emergence traps: 276 to 97 888 individuals m^{-2} $night^{-1}$; re-entry traps: 3137 to 103 666 individuals m^{-2}) generally were within reported ranges. The closest comparisons could be made to a study in the lagoon of Heron Reef, Great Barrier Reef (Jacoby & Greenwood 1988). The number of zooplankters captured in Moreton Bay was an order of magnitude greater for most taxa. Past studies have concentrated on the importance of demersal zooplankton in the trophic webs of coral reefs, but this assemblage may be equally important in estuaries.

All types of sampling used in this study were effective, but each also appeared to have biases. Net tows at the surface tended to capture smaller forms and missed many demersal taxa, even at night. These results indicated that most animals did not move to the surface of the 1 to 4 m water column or some taxa avoided the net. Re-entry traps and emergence traps captured equal numbers of 19 out of 42 taxa. Eight groups, mainly larger demersal zooplankters and crawling gastropods,

Table 10. Occurrences of statistically significant temporal emergence patterns within season/lunar period/substratum. Peaks in emergence greater than 10 zooplankters m^{-2} $90min^{-1}$ Su: summer; Wi: Winter; FQ: first quarter; FM: full moon; LQ: last quarter; NM: new moon; Co: coral; Gr: grass; Mu: mud; –: no effect for levels of this factor; – –: emergence pattern not shown by this taxon; cop.: copepodites

Taxon	Sunset	Nocturnal	Sunrise	Bimodal	Diurnal
Pseudodiaptomus colefaxi ♂♂	Su/FQ/Gr Su/LQ/Gr Su/LQ/Mu Wi/FQ/Gr Wi/FQ/Mu Wi/FM/Co Wi/FM/Mu Wi/LQ/Gr Wi/LQ/Mu	Su/FQ/Co Su/FM/Co	– –	Su/FM/Mu Su/NM/Gr Wi/Nm/Mu	– –
P colefaxi ♀♀	Wi/FM/Co Wi/FM/Mu Wi/LQ/Mu	– –	– –	– –	– –
P. colefaxi ovigerous ♀♀	Su/LQ/Gr Wi/FQ/Gr Wi/FQ/Mu Wi/FM/Co Wi/FM/Mu Wi/LQ/Gr	Su/FM/Gr Su/FM/Mu	– –	Su/LQ/Mu Su/NM/Gr	– –
P. colefaxi cop.	Wi/FQ/Gr Wi/FM/Co Wi/FM/Mu	Su/FM/Mu	– –	– –	– –
Pseudodiaptomus mertoni ♂♂	Su/FQ/Gr Su/FM/Co Su/FM/Gr	Su/FQ/Co	– –	– –	– –
P mertoni ♀♀	Su/FQ/Gr Su/FM/Co Su/LQ/Gr	Su/FQ/Co	– –	– –	– –
P. mertoni cop.	– –	Su/FQ/Co – –	– –	– –	Su/FM/Gr
Stephos spp.	Wi/QF/Gr	Wi/FM/Gr	– –	– –	– –
Acartia sp. adults	– –	– –	– –	– –	Su/LQ/Co
Pseudocyclops spp	Su/FM/Co Wi/NM/Co	– –	– –	– –	– –
Ridgewayia sp.	– –	Su/FM/Co	– –	Su/LQ/Co	– –
Miscellaneous calanoids	– –	– –	– –	– –	Su/FQ/Co Su/FQ/Mu
Oithona spp	– –	– –	– –	– –	Su/FQ/Mu
Miscellaneous harpacticoids	– –	– –	– –	– –	Su/FQ/Mu
Copepod nauplii	– –	– –	– –	– –	–/–/Co –/–/Gr
Amphipods	Su/LQ/Co Su/NM/Co Wi/FQ/Co Wi/FM/Co Wi/FM/Mu Wi/LQ/Co	– –	– –	– –	– –
Cumaceans	Su/FQ/Gr Su/FM/Co Su/FM/Gr Su/LQ/Co Su/LQ/Gr Wi/FQ/Gr Wi/NM/Gr	– –	– –	– –	– –
Mysids	Su/FM/Co Su/FM/Gr Su/LQ/Co Su/LQ/Gr Su/NM/Co Su/NM/Mu Wi/LQ/Mu Wi/NM/Gr	– –	– –	– –	– –
Ostracods	Wi/FQ/–	– –	– –	– –	– –
Caridean/anomuran larvae	– –	Su/FM/Co Su/FM/Mu Su/NM/Gr Su/NM/Mu	– –	– –	– –
Zoeae	– –	–/FQ/Co	– –	– –	– –
Megalopa	Su/FM/Gr	– –	– –	Wi/NM/Mu	– –

Table 10 (continued)

Taxon	Sunset	Nocturnal	Sunrise	Bimodal	Diurnal
Sagitta spp.	--	--	--	--	Su/FQ/Co Su/LQ/Co
Larvaceans	--	--	--	--	Su/LQ/Co
Polychaetes	Su/FQ/Gr Wi/FQ/Co Wi/FQ/Gr Wi/FQ/Mu	Su/NM/Gr Wi/LQ/Col	Su/NM/Co	Su/LQ/Co Wi/LQ/Gr	--
Polychaete larvae	--	--	--	--	Wi/--/--
Gastropod veligers	--	--	--	--	All
Bivalve veligers	--	Su/FM/Co	--	--	--

Table 11. Distribution of significant night-time emergence patterns with peaks of more than 10 individuals m^{-2} $90min^{-1}$ among levels of factors in ANOVAs

Factor	Level	No. of significant night-time emergence patterns
Season	Summer	48
	Winter	36
Lunar period	First quarter	22
	Full moon	29
	Last quarter	20
	New moon	14
Substratum	Coral	32
	Grass	31
	Mud	21

were more common in re-entry trap samples. These 8 taxa (i.e. *Pseudodiaptomus colefaxi* copepodites, *Peltidium* spp., amphipods, cumaceans, ostracods, polychaetes, carideans, and gastropods) were nearer the bottom during the day than the 15 groups caught in greater numbers in emergence traps. These 15 taxa, which apparently were near the bottom but did not enter defaunated sediment, included 5 groups of small demersal zooplankton (*Stephos* spp., *Pseudocyclops* spp., *Ridgewayia* sp.; *Parategastes* sp. and *Spadella cephaloptera*), 3 non-demersal adult taxa (*Parvocalanus* sp., *Metis holothuriae*, and larvaceans), and 7 larval taxa (miscellaneous nauplii, zoeae, caridean/anomuran larvae, megalopa gastropod veligers, bivalve veligers, and tunicate larvae). All 43 taxa were caught in RETs and had to move at least 70 cm into the water column to be trapped. These results contradict hypotheses that re-entry traps consistently yield an order of magnitude more zooplankters than emergence traps (Alldredge & King 1980) and that smaller zooplankters tend to remain nearer the bottom (Alldredge & King 1985). All of these conclusions agree with observations from a study at Heron Reef made by Jacoby & Greenwood (1988).

Re-entry traps did not show a consistent increase in numbers of colonizers over a 3-night period. This agrees with the findings of Bell & Devlin (1983), Chandler & Fleeger (1983), and Jacoby & Greenwood (1988) but differs from results reported by Stretch (1985) and Virnstein & Curran (1986). Colonization may have decreased after one night or immigration may have been balanced by emigration. Density-dependent movement which should lead to stable levels of colonizers has been observed in amphipods and meiofauna (Ambrose 1986, Service & Bell 1987).

Variation in zooplankton numbers attributed to seasons was more pronounced in Moreton Bay than in the lagoon of Heron Reef (Jacoby & Greenwood 1988). In Moreton Bay, 25 out of 32 taxa of adults were taken in greater numbers in the summer in contrast to 13 out of 23 taxa at Heron Reef. At both locations, most larval taxa were captured in greater numbers in the summer (Moreton Bay: 10 out of 14 taxa; Heron Reef: 8 out of 10 taxa) indicating a summer peak in reproductive activity as has been reported elsewhere (Sale et al. 1976, 1978, McWilliam et al. 1981). Moreton Bay was expected to have stronger seasonality due to greater changes in abiotic factors, e.g. temperature, salinity, and daylength.

Lunar effects on emergence were less clear in Moreton Bay than at Heron Island (Jacoby & Greenwood 1988). Significant temporal peaks in emergence were distributed more evenly among lunar periods for taxa from Moreton Bay. At Heron Reef, most demersal taxa (16 out of 19) emerged in greater numbers during a lunar period with part of the night moonless, but this trend was less apparent in Moreton Bay (10 out of 17 taxa). Most of the demersal taxa emerging in large numbers during the full moon in Moreton Bay, e.g., *Pseudodiaptomus colefaxi*, *Pseudocyclops* spp., and *Ridgewayia* spp., were smaller than the other demersal groups. Unexpectedly, amphipods and cumaceans, relatively large animals, displayed approximately equal emergence in all lunar periods at both locations. At both places, ca 40 % of the non-demersal adult taxa and 80 % of the larval taxa emerged in large numbers during the full moon.

Previous work indicated variable effects of lunar period on emergence (Alldredge & King 1980, 1985, Ohlhorst 1982). Tidal flux may have altered emergence behavior (Palmer & Brandt 1981, Eckman 1983, Hicks 1986, Palmer 1986), but some zooplankters emerged during all states of the tide in Moreton Bay, at Heron Reef (Jacoby & Greenwood 1988), and at other sites (Grindley 1972, Pillai & Pillai 1973). Turbidity in Moreton Bay generally was high and may have reduced the effect of moonlight on emergence much as darkened emergence traps did in a study by Alldredge & King (1980). In spite of these complications, many demersal taxa emerged in greater numbers during lunar periods in which part of the night was moonless. Visual predation in the water column should be reduced during moonless portions of the night. Larval forms and small or transparent adult zooplankters emerged mainly during full and new moon periods or showed no effect of lunar period on emergence. These taxa may not be less subject to visual predation because of their size and lack of coloration, but they may accrue increased dispersal on spring tides.

Most taxa in this study (95 %) emerged in greatest numbers from coral or grass, the 2 structurally complex substrata. This trend is corroborated by results from a variety of other studies indicating that structure is often correlated with enhanced densities of animals (Alldredge & King 1977, Porter et al. 1977, Coull et al. 1979, Feeley et al. 1979, Stoner 1980, McWilliam et al. 1981, Alldredge 1985, Stoner & Lewis 1985, Hicks 1986, Palmer 1986, Jacoby & Greenwood 1988). The substrata in this study were not limited exclusively to one type of bottom, therefore, taxa from coral may have been in the surrounding rubble and taxa from grass may have been in the underlying mud. The presence of any structure above the bottom has been observed to lead to greater numbers of animals, possibly due to increased food, decreased water flow, protection from predators, or behavioral choice (Hicks 1977, Nelson 1979, Ravenel & Thistle 1981, Stoner 1982, Coull & Wells 1983, Edgar 1983, Thistle et al. 1984, Leber 1985, Kern & Taghon 1986, Palmer 1986, DeWitt 1987).

By definition, daylight has a major effect on the behavior of demersal zooplankton (Jansson & Källander 1968, Alldredge & King 1980, Tranter et al. 1981, Walter et al. 1981, Ohlhorst 1982, Youngbluth 1982b, Renon et al. 1985, Bell et al. 1986, Walters & Bell 1986, Jacoby & Greenwood 1988). In this and other studies, emergence predominately occurred at night. Temporal patterns in emergence exhibited by some taxa were limited to restricted periods of time and varied among different sets of samples (Jacoby & Greenwood 1988, this study). Emergence during restricted periods of the night will limit exposure to predation, but it also increases the likelihood of contacting a mate. Copepods, amphipods, cumaceans, and other taxa may rely on this behavior to increase the relative concentrations of conspecific individuals and sexual pheromones in the water column (Katona 1973, Griffiths & Frost 1976, Lyes 1979, Jacoby & Youngbluth 1983). The correspondence observed between diel emergence patterns of both sexes in the same species during different seasons and lunar periods supports this hypothesis (Jacoby & Greenwood 1988, this study).

Emergence traps and re-entry traps rely on behavior of zooplankters for an assessment of abundance. Both types of traps appear to underestimate the total densities of zooplankters, but they have been reported to accurately reflect relative differences in abundance (Alldredge & King 1980, Stretch 1985). Results of this study and that by Jacoby & Greenwood (1988) indicate that conclusions regarding zooplankton abundance based on catches in re-entry and emergence traps must include an appreciation of behavioral variability.

Seasonality in emergence probably was due primarily to changes in abundance because increases in captures within taxa were consistent among lunar periods and substrata. In addition, these differences were more pronounced in the harsher environment of Moreton Bay. A seasonal peak in mating may have added a behavioral affect to the seasonality of emergence.

Substratum-related variations in emergence were consistent through all seasons and lunar periods and were seen between samples taken on the same night. These results indicated that these variations were due to stable differences in abundance, not substratum-related behavioral effects on emergence. A behavioral choice of substratum may have contributed to the observed distributions.

In contrast, diel and lunar variations in catch rates were probably a result of behavioral changes, because lunar trends were not dependent on the order in which the moon phases were sampled and these effects were less obvious in Moreton Bay where turbidity reduced penetration of moonlight into the water column. In addition, samples from consecutive lunar periods typically were spaced over a 1 mo interval which should have reduced the effect of changes in abundance. Variations in abundance of the magnitude required to generate the observed diel patterns in emergence are unlikely in 1 d. These patterns probably result from behavioral changes and appear to have been a response to illumination.

Results of work in Moreton Bay and at Heron Reef (Jacoby & Greenwood 1988) suggest that it may be necessary to view demersal zooplankton as an assemblage composed of at least 2 types of animals. One group would include animals that primarily are benthic but emerge into the water column on a regular basis. A second category would include relatives of holoplankters that move to the bottom during the daytime.

Benthic, demersal taxa (e.g. *Peltidium* spp., *Parategastes* sp., amphipods, carideans, cumaceans, isopods, ostracods, tanaids, polychaetes, and *Spadella cephaloptera*) probably feed while in or on the bottom. These groups, for example amphipods and cumaceans, would be very near the bottom during the day as shown by a tendency to be captured in re-entry traps (Jacoby & Greenwood 1988, this study). Emergence would not vary significantly among lunar periods (Alldredge & King 1980, 1985, Ohlhorst 1982, Jacoby & Greenwood 1988, this study) because only small percentages of the populations of these animals would emerge to mate or disperse (Jones 1963, Mills 1967, Anger & Valentin 1976, Edgar 1983, Ambrose 1986). These taxa may not rise very far into the water column and may escape net tows at the surface (Jacoby & Greenwood 1988, this study). These benthic, demersal taxa often are subject to heavy predation by fishes feeding on the bottom during the day (Alheit 1981, Choat 1982), therefore, nocturnal, visual predators may not exert a significant selective force even if aided by moonlight. Predation may not be as strong a selective force as the need to find a mate or disperse.

The planktonic category of demersal zooplankton would include calanoid copepods (*Pseudodiaptomus, Stephos, Pseudocyclops,* and *Ridgewayia*) and mysids. Animals in these taxa probably feed (Hart 1977), mate, and disperse in the water column like their holoplanktonic relatives. A greater percentage of the populations of these zooplankters would be expected to migrate each night. These groups may move closer to the surface at night and may swarm near but not settle on or in the substratum during the day (Emery 1968, Hamner & Carleton 1979). These behaviors would lead to their capture in night-time net tows and in daytime net tows that sampled near the bottom and to their rarity in re-entry traps (Greenwood 1977, Jacoby & Greenwood 1988, this study). Visual predation on these taxa may be reduced if they remain near the substratum during sunlit or moonlit periods (Zaret & Suffern 1976, Robertson & Howard 1978, Fancett & Kimmerer 1985). Studies of these taxa should provide clearer answers to questions concerning visual predation and the evolution of the demersal habit.

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