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Title: Migration of demersal plankton at Double Reef, Guam, in relation to lunar phase and substrate

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Steven S. Amesbury, Chairperson, Thesis Committee

In this study, mobility of demersal plankton in relation to substrate and lunar phase (new moon and full moon) was tested. Assemblages were collected from reentry traps that held different substrates: sand, coral rubble, and an artificial substrate. These were deployed at Double Reef, Guam, Mariana Islands. Significantly different numbers of cyclopoids, harpacticoids, and ostracods entered the three substrates. Cyclopoid and harpacticoid copepods were found in significantly different numbers between the full moon and the new moon. A significantly larger proportion of both cyclopoid and harpacticoid copepods resettled in their substrate of origin when given the choice to resettle in either sand or coral rubble. Observations of live demersal plankton obtained from sand cores revealed that harpacticoids and ostracods primarily crawled and that cyclopoids primarily swam or flitted. All harpacticoids and many of the cyclopoids originating from sand were able to find shelter in the interstitial spaces either by burrowing, in the case of harpacticoid copepods, or by finding a space large enough to swim into, in the case of the cyclopoid copepods. Most cyclopoid and harpacticoid copepods originating from coral rubble were unable to find shelter. These results suggest that demersal plankton will discriminate between substrates and that behavioral and morphological characteristics are responsible for the plankters choice of shelter. Although they are subject to the currents in the water column, the demersal plankton can control their diel settlement, and are thus not truly planktonic. The term "paraplankton" is proposed to describe these organisms.

TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

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MIGRATION OF DEMERSAL PLANKTON AT DOUBLE REEF, GUAM, IN RELATION TO LUNAR PHASE AND SUBSTRATE

By

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INTRODUCTION

In this study, I examined settlement behavior of demersal plankton relative to lunar phase and substrate type. The timing of emergence and the distance demersal plankton migrate above the bottom has been shown to vary with the lunar phase (Alldredge and King, 1980, 1985). I examined whether the likelihood of demersal plankton emerging into the water column will also vary between the new moon and full moon. If visual predation is an important factor in the migration of demersal plankton, then there should be more demersal plankton in the water column on the new moon than on the full moon. Different assemblages of demersal plankton reportedly emerge from different substrates (Alldredge and King, 1977; Porter and Porter, 1977; Porter *et al.*, 1977). I investigated whether the variety of emerging assemblages was a reflection of what settled in the substrate. This is a question of whether demersal plankton settle randomly, exiting the water column on cue without regard to location, or if demersal plankton are able to distinguish between substrates, selecting a preferred shelter.

Whereas most plankton are free-floating organisms, either weak swimmers or passive drifters, many are capable of some active motility. Both phytoplankton and zooplankton exhibit diel vertical migration. Demersal plankton migrate daily between the bottom and the water column. Relatively little is known about the factors that influence their migrations. Previous studies have shown how demersal plankton assemblages vary depending upon which section of a reef is sampled, e.g. flat, lagoon, channel, slope (Birkeland and Smalley, 1981), and over what substrate they have been collected

(Alldredge and King, 1977; Porter and Porter, 1977; Porter *et al.*, 1977). Moon phase has also been shown to affect the migration of plankton (Alldredge and King, 1980, 1985; Jacoby and Greenwood, 1988).

Alldredge and King (1980; 1985) found variances in the timing of migration by demersal plankton. Some taxa migrated on a consistent schedule, some other taxa migrated on a consistent schedule except during specific periods in the lunar cycle, and another group of taxa did not follow a schedule, instead, emerging only when it was dark. Larger organisms had a greater tendency to avoid light (Alldredge and King, 1980). Unless they have special adaptations to reduce their visibility, such as a transparent body, larger organisms are easier for visual predators to detect. However, it is equally difficult to detect visually a large plankter as a small one when there is no light. Thus, avoiding light would decrease the vulnerability of large demersal plankton to visual predation. This suggests that avoidance of visual predation is an important factor in the timing of migrations (Alldredge and King, 1980, 1985; Hobson and Chess, 1979).

Samples of demersal plankton vary depending upon the type of substrate over which they were collected (Alldredge and King, 1977; Porter and Porter, 1977; Porter *et al.*, 1977). Alldredge and King (1977) and Porter *et al.* (1977) found that the number of plankters collected increased with the size of the interstitial space of the substrate. Alldredge and King (1977) concluded that the density of demersal plankton communities depends on the heterogeneity in interstitial space of the substrate. Substrate is important to demersal plankton, as it determines whether the plankton can find shelter and safety from predation. Different substrates will provide interstitial spaces of various sizes, will have different volumes of interstitial space, and will vary in the ease of burrowing for demersal plankton seeking temporary shelter.

It is unknown whether demersal plankton can differentiate between substrates or if they simply enter whichever substrate is beneath them at the time they choose to exit the water column. The difference in planktonic assemblages emerging from specific substrates (Alldredge and King, 1977; Porter and Porter, 1977; Porter *et al.*, 1977) indicates that there are processes by which demersal plankton select the substrate in which they settle. The selection may be passive, in which particular plankters are incapable of finding shelter in some types of substrates, or active, in which a plankter chooses a preferred substrate. For example, plankton attempting to settle in an improper substrate may be left exposed and consumed by predators. Alternately, the settling demersal plankton continue drifting or swimming until they find suitable shelter.

In addition to substrate and lunar phase, previous studies have found multiple factors that affect demersal plankton. Birkeland and Smalley (1981) found that abundance and taxanomic composition depended upon where on a reef the plankton were collected. Hobson and Chess (1979) found differences between day and night abundances of demersal plankton. Lewis and Boers (1991) found that demersal plankton abundances changed seasonally. Carleton *et al.* (2001) found that the presence of reef plankton communities at any location was determined by the local currents and, to a lesser extent, by the behavior of the individual taxa.

The majority of studies on demersal plankton used emergence traps to collect samples. Alldredge and King (1980) introduced reentry traps as an alternative to emergence traps. These traps were simply polyethylene boxes containing sun-dried beach sand, cleaned of microfauna. As demersal plankton reenter the substrate from the water column, they are collected by the reentry traps.

The performance of reentry traps in sampling demersal plankton communities was tested by Stretch (1985), Madhupratap *et al.* (1991), and Cahoon and Tronzo (1988). Stretch (1985) used an air lift dredge to collect organisms in the sand and compared these samples to the demersal plankton he caught in reentry traps. Madhupratap *et al.* (1991) designed a tool that took sand cores and compared populations from the cores to assemblages from reentry traps. In both studies, the authors found that the assemblages caught in reentry traps closely matched the composition of those taken from the alternate devices, although the estimates for the numbers of plankters per unit area were less. Cahoon and Tronzo (1988) compared assemblages taken from reentry traps and from emergence traps and found them to differ significantly. The traps targeted different taxa, and the reentry traps collected more individuals. They concluded that reentry traps are good tools for studying demersal plankton.

Alldredge and King (1980) noted the difficulty of reproducing certain substrates in reentry traps, such as coral colonies and pavement. Because of this difficulty, substrates in reentry traps have been limited to sand and gravel. Placement of the traps has been limited to sand and gravel substrates for the same reason (Alldredge and King, 1980, 1985; Stretch, 1985; Cahoon *et al.*, 1995; Cahoon and Tronzo, 1988, 1990, 1992; Madhupratap *et al.*, 1991). On tropical coasts, sand is only one type of substrate; other important substrates include live coral, pavement, and rubble.

The reentry traps in this study held three different substrates to test demersal plankton substrate choice during settlement. These substrates were sand, coral rubble, and an artificial substrate. In addition, the behavior of demersal plankton was examined to determine how a substrate was chosen.

MATERIALS AND METHODS

Reentry Traps

This study was conducted at Double Reef (13°35.89' N, 144°50.14' E), a patch reef located approximately 300 m off of the western, leeward shore of Guam, Mariana Islands. Traps were placed at a depth of 9 m in a sand pit located between the patch reef and the fringing reef. Traps were deployed during the afternoon, within two days of the new or full moon.

Sampling began on 8 March 2001, two days before the full moon. Further samples were taken every two weeks until three sets of samples were collected from around both the full moon and the new moon. There were five replicates of reentry traps per deployment, with three traps in a replicate, for a total of 15 traps. To test if demersal plankton could differentiate between substrates, the three traps of each set held a different substrate: one liter of sand (Hawaiian Rock manufactured sand), coral rubble (*Pocillopora elegans* and *P. eydouxi*) stacked to the lip of a trap, and an artificial substrate constructed from stripping pads cut to fit the trap and stacked three high (3M #8550, "Doodlebug"; J. Robinson, pers. comm., 2000) with 0.9 kg of lead shot in a plastic storage bag (Presto, 0.94 ℓ) for ballast. Sand grains were between 250 μm to 1 mm in diameter. Sand and coral rubble were chosen as substrates because they occur naturally on coral reefs. The stripping pads were chosen to test how effective they would be as an artificial substrate. The bodies of the traps were 17 x 17 x 7 cm polyethylene containers (Rubbermaid #3871) with sealable lids. Each held a volume of 1.32 ℓ. Thirty samples were taken with each substrate; a total of 90 samples was taken.

Prior to transport to the site, each trap was filled with 90-µm filtered seawater and sealed (Cahoon and Tronzo, 1990). Traps were transported in coolers to minimize temperature differences en route. At the site, traps were placed in predetermined positions within the pit. Traps from one set were placed adjacent to each other, and then their lids were removed.

The traps were collected and processed the following morning. To minimize contamination by holoplankton, the lids were set by sliding them over the opening and then sealing them on the trap. The traps were placed in coolers for the return trip to maintain temperatures and to minimize mortality and decomposition during transportation. Plankton were extracted from sand traps and coral rubble traps by rinsing the substrate with fresh water (Cahoon and Tronzo, 1988, 1992). The osmotic shock caused the zooplankton to relax, and turbulence kept them in the water column for a short time. The supernatant water was decanted through a Nitex 90-µm mesh filter. The traps were rinsed with fresh water six times or until no plankton could be seen. The artificial pads were rinsed under a stream of water for at least 20 seconds, and then the rinse water was filtered through the Nitex 90-µm mesh filter. This method was chosen because the complex structure of the pad would make it difficult to remove organisms by floating them to the surface. The samples were then preserved in 5% buffered seawater-formalin.

Plankton were identified by gross morphology and counted. The dominant zooplankton were crustaceans: amphipods, cyclopoid copepods, harpacticoid copepods, isopods, and ostracods. The cyclopoid, harpacticoid, and ostracod counts were compared by regression analysis to determine if there were any correlations in numbers between these three taxa. A two-way, fixed-factor ANOVA was then used to determine whether substrate or lunar phase significantly affected abundance. The data were corrected for zeros by adding 0.5 to each count, then natural log transformed to normalize the data.

Substrate Choice

Plankton samples were obtained from both sand and coral rubble. Samples from sand were acquired by taking a shallow core of sand with 414-mℓ round plastic containers ("Ziploc", S.C. Johnson & Son, Inc.) with an opening diameter of 13 cm. The first 11 samples were taken from a sand pit located at the northern end of Pago Bay. Waves created by Typhoon Halong moved rubble onto the sand pit, however, so the last three samples were taken from Double Reef. Nine samples from coral rubble were acquired with reentry traps left in the field overnight. The cores from Pago Bay were flushed with fresh water for approximately 20 seconds; Double Reef and coral rubble samples were flushed with 9 ℓ of 90–μm filtered sea water. The supernatent water was filtered through the same mechanism described for the reentry traps. The contents of the filter were then transferred to the substrate enclosures.

The inner dimensions of the enclosures were 7.6 x 21.2 x 21.2 cm (H x W x D). Each enclosure held two substrate chambers, one filled with sand to a depth of 2 cm, and the other contained coral rubble set on a platform raised 2 cm above the bottom. This configuration created a level surface over which plankton could easily move between the chambers. The substrate chamber had the inner dimensions of 7 x 20 x 8.5 cm, with an additional 1.5 cm in depth for the partitioning structure. These dimensions were calculated to have a surface area greater than that of the sand cores. The substrate chambers were sealed two hours after introducing the plankton. The plankton were then removed and preserved following the same methods used above for the reentry trap samples.

Cyclopoid and harpacticoid copepods were counted, and the counts were converted to proportions. Other taxa were not examined because they were absent from several samples. The proportions of individual taxa were calculated between the substrates. Proportions were arcsine-transformed to obtain a normal distribution, and then compared by a two-way ANOVA, with taxa and substrate as the factors. Data for plankters originating from sand and rubble were analyzed separately.

Behavioral Observations

Plankton were extracted from sand cores that were obtained with the same procedures used in the substrate choice test by flushing the sand with 3 ℓ of 90-µm filtered seawater. Live organisms were placed in glass dishes with a small amount of sand from the cores and observed immediately after all the cores had been processed. Samples were examined for any visible fauna in the water column, on the sand, and in the sand. The samples were placed in a dark enclosure for one hour and then reexamined. The organisms were scored by taxon and by behavior. Behavioral categories were assigned on the basis of preliminary observations.

The behavior categories were swimming, flitting, crawling, digging, and motionless. Swimming occurred when plankton were in motion within the water column and did not head immediately towards the bottom. Flitting behavior was defined as short bursts of swimming interspersed with either crawling or remaining motionless. Flitting usually began on the bottom and then continued up into the water column before returning to the bottom, but also included individuals who swam along the bottom. Crawling organisms moved along the bottom of the dish and did not display any other form of locomotion. Digging organisms were those that attempted to bury themselves in the substrate. The organisms classified as motionless did not change position unless disturbed by contact.

Sand Entry Tests

Plankton for the entry experiments were obtained with the same procedures used for the choice test samples from Double Reef. Both sand and coral rubble samples were taken. Each collection was then transferred to a glash dish 5.5 cm in diameter glass dish. Individual cyclopoids and harpacticoids were transferred into a 1.5-cm diameter cap containing a thin layer of manufactured sand. The individuals were recorded with a dissecting microscope (Wild Makroskop M420) fitted with a video camera (Sony DXC-151) attached to a Hi-8 recording deck (Sony EV-S7000 NTSC). The copepods were observed until they found shelter in the sand or until approximately 90 seconds had passed. From the recording, the copepods were timed and scored as whether they were able to hide in the sand. The copepods were divided into the categories of cyclopoid and harpacticoid copepods originating from either sand or coral rubble. Differences between categories and sub-categories were examined with a *G*-test of independence computed with a William's correction (Sokal and Rohlf, 1995).

RESULTS

Reentry Traps

The reentry traps captured a wide range of organisms, of which crustaceans were the most abundant (Table 1; Figure 1a). The majority of crustaceans was, in decreasing order of abundance, cyclopoid copepods, harpacticoid copepods, ostracods, isopods, amphipods, and mysids. Other crustaceans included calanoid copepods, brachyurans and brachyuran megalopa, cumaceans, unidentified nauplii, tanaeids, and unidentified crustaceans. There was also a large number of diatoms and foraminiferans. Chaetognaths, juvenile gastropods, nematodes, and polychaete worms were frequently observed, but they were not as prevalent as the major crustaceans. Medusae, eggs, flatworms, juvenile bivalves, juvenile fish, juvenile urchins, siphonophores, and tintinnids were rarely found. There was also a large number of unidentified organisms, that range from ubiquitous to rare.

Table 1: Mean number per trap and percent frequency of organisms.

Taxa	Mean Number per Trap	Percent Frequency
Amphipod	1.98 ± 0.16 SE	84.4
Anthomedusa	0.13 ± 0.04 SE	12.2
Brachyuran	0.09 ± 0.02 SE	7.8
Chaetognath	0.66 ± 0.11 SE	36.7
Miscellaneous crustaceans	0.90 ± 0.08 SE	44.4
Copepod, calanoid	0.39 ± 0.08 SE	25.6
Copepod, cyclopoid	70.18 ± 1.23 SE	100.0
Copepod, harpacticoid	55.13 ± 0.84 SE	100.0
Cumacean	0.51 ± 0.06 SE	36.7
Diatom	20.98 ± 2.02 SE	88.9
Miscellaneous eggs	1.48 ± 0.37 SE	40.0
Flatworm	0.04 ± 0.02 SE	3.3
Foraminiferan	9.21 ± 1.62 SE	76.7
Isopod	3.39 ± 0.14 SE	81.1
Miscellaneous juveniles	2.48 ± 0.18 SE	72.2
Mysid	0.76 ± 0.07 SE	41.1
Nauplius	0.26 ± 0.06 SE	21.1
Nematode	1.58 ± 0.20 SE	65.6
Ostracod	9.68 ± 0.31 SE	96.7
Polychaete	1.41 ± 0.19 SE	60.0
Siphonophore	0.03 ± 0.02 SE	3.3
Tanaeid	0.72 ± 0.13 SE	37.8
Tintinnid	0.02 ± 0.02 SE	2.2
Miscellaneous unknowns	11.99 ± 0.30 SE	96.7

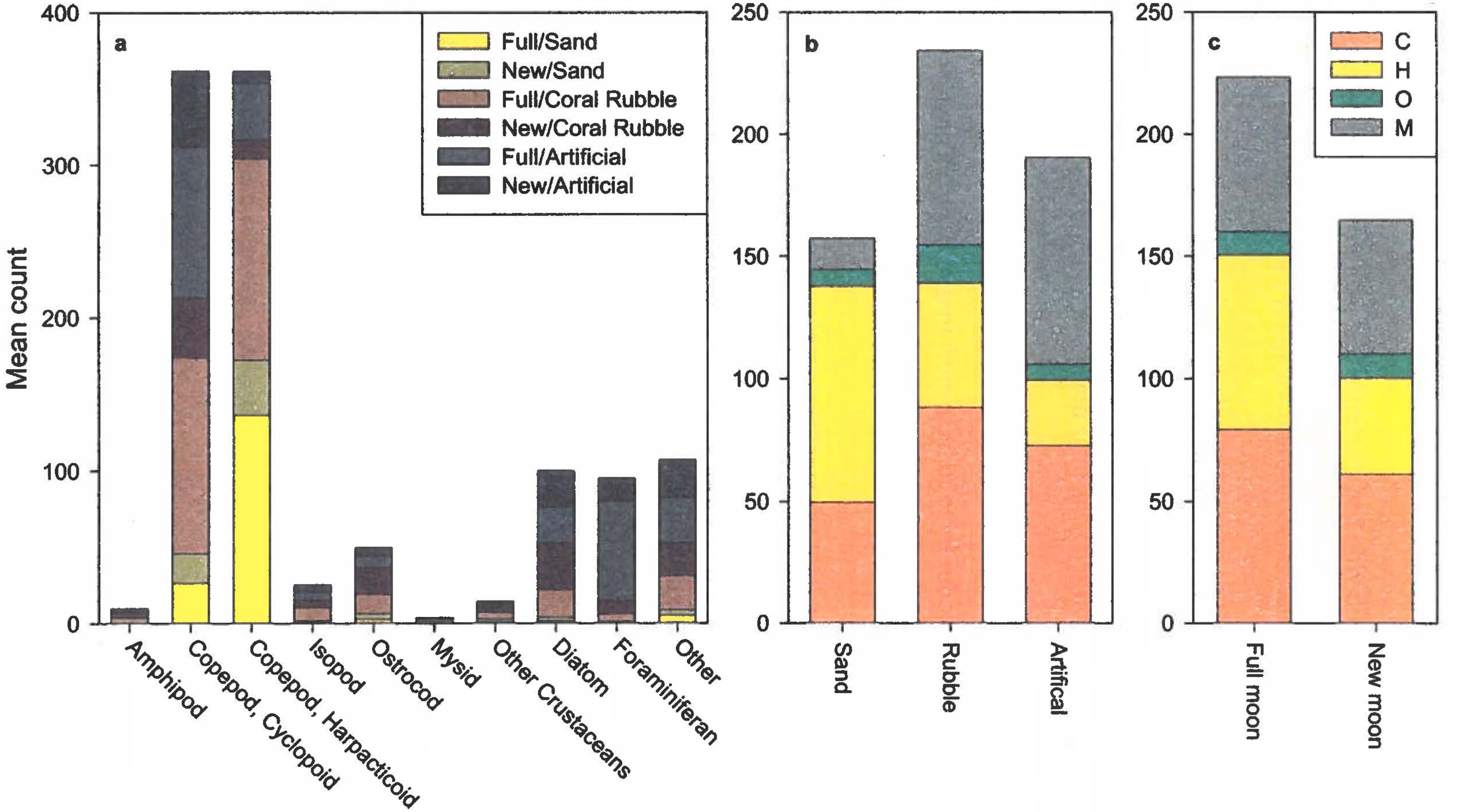

Figure 1: Mean counts per month by taxa and per trap by substrate and lunar phase. (a) stacked mean counts of organisms with the greatest representation in reentry traps (n = 90). Rare crustaceans are lumped into the group "Other Crustaceans" and other rare organisms and unknwons are lumped into the category "Other;" (b) mean numbers of organisms found in reentry traps in each of the three substrates (n = 30); (c) mean number of organisms found in reentry traps during the full and new phases of the moon (n = 45). ***Legend (b, c):** 'C' = mean number of cyclopoids per trap; 'H' = mean number of harpacticoids per trap; 'O' = mean number of ostrocods per trap; 'M' = mean number of miscellaneous organisms per trap.

Cyclopoid and harpacticoid copepods were the only organisms that were represented in every sample, and ostracods had only three counts of zero in the 90 samples. Abundances of cyclopoids, harpacticoids, and ostracods in the traps were not significantly correlated, indicating that each taxon settled independently of the other taxa.

Different numbers of organisms entered the three substrates (Table 2; Table 3; Figure 1b). Fewer organisms entered sand and significantly more entered the coral rubble. An intermediate number of organisms settled in the artificial substrate, but this was not significantly different from sand or coral rubble.

Table 2: Means and standard errors (SE) of the total number of organisms found separated by lunar phase and substrate. Letters in parentheses indicate significant difference between groups. 'A' and 'B' are used for comparisons of substrate and lunar phase. 'C' and 'D' are used for just substrate, and 'E' and 'F' are used for comparisons between the full moon and the new moon. Differences were tested for by the SNK post-hoc test.

	Full Moon	**New Moon**	**Total**
Sand	182.3 ± 29.6 SE (A)	132.3 ± 32.5 SE (A)	157.3 ± 22.1 SE (C)
Coral Rubble	276.2 ± 26.1 SE (B)	257.6 ± 32.4 SE (AB)	266.9 ± 20.5 SE (D)
Artificial Pad	211.3 ± 23.2 SE (AB)	214.5 ± 24.2 SE (A)	212.9 ± 16.5 SE (CD)
Total	223.3 ± 16.1 SE (E)	201.5 ± 18.6 SE (F)	

Table 3: Summary of results for 2-way ANOVAs comparing abundances. Factors are named above the categories. Data are mean number of plankters per trap followed by the F statistic for the comparison. Numbers in parenthesis are the n for the comparison.

	Lunar Phase (45)			**Substrate (30)**				**Interaction**
Taxa	**Full**	**New**	**F**	**Sand**	**Rub.**	**Art.**	**F**	**F**
All	182	132	7.13**	157	267	213	4.57*	0.35
Cyclopoid	79	61	4.17*	50	88	73	5.08**	0.15
Harpacticoid	71	39	12.17***	88	51	27	12.08***	1.92
Ostracod	9	9	0.35	7	16	7	15.69***	1.52

* = p > 0.05, ** = p > 0.01, *** = p > 0.001

Individually, the three taxa also differed numerically between the substrates (cyclopoid: $p < 0.01$, harpacticoid: $p < 0.001$, ostracod: $p < 0.01$; Table 3). Cyclopoid copepods entered the coral rubble and artificial pad traps in significantly higher numbers than in the sand traps (Student-Newman-Keuls Multiple-Comparison Test, SNK, at $p < 0.05$; Figure 2a). Harpacticoid copepods were most numerous in the sand traps, less numerous in the coral rubble traps, and least abundant in the artificial pad traps (SNK at $p < 0.05$; Figure 2b). The greatest number of ostracods was found in coral rubble traps, but the numbers in sand and artificial pad traps did not differ significantly (SNK at $p < 0.05$; Figure 2c).

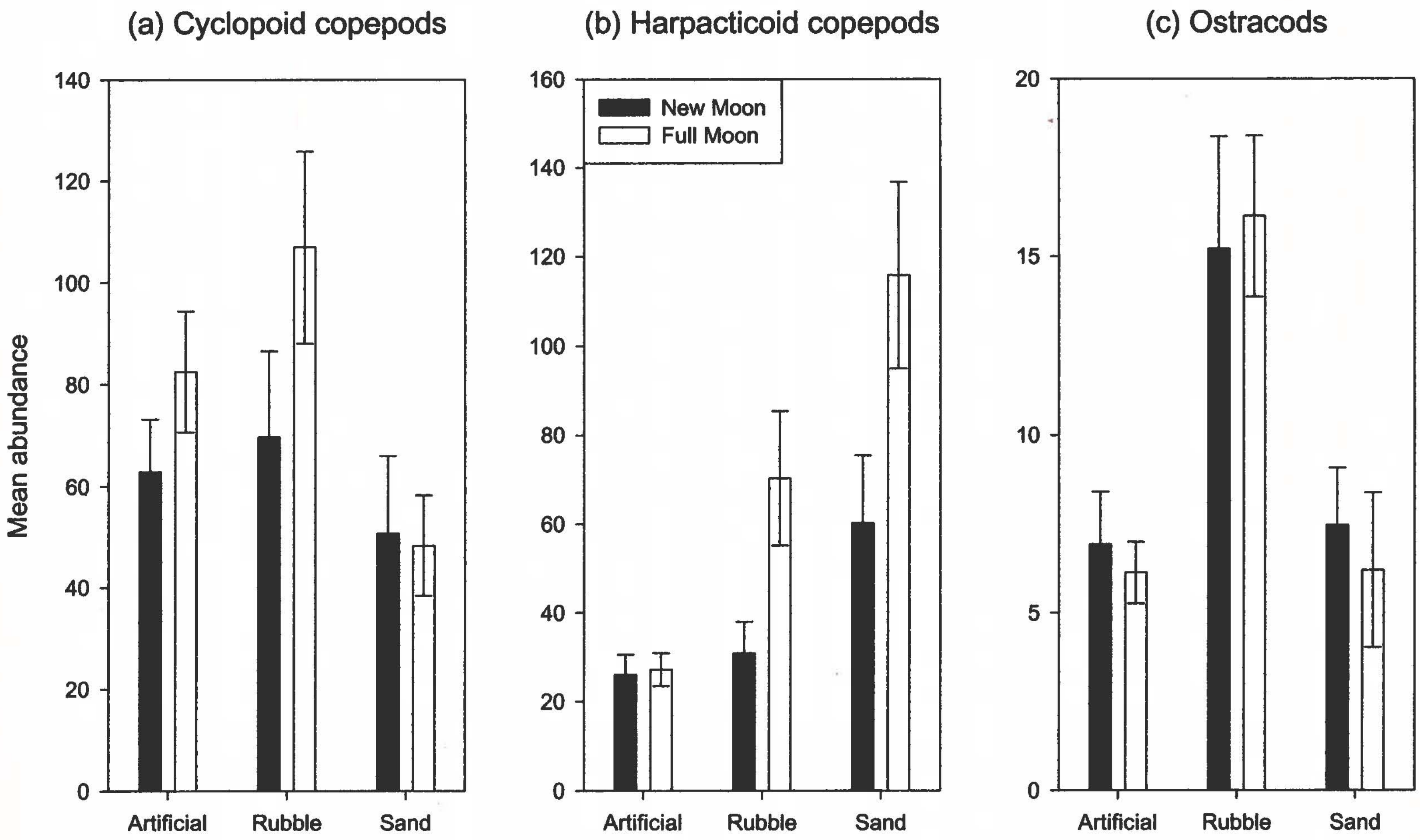

Figure 2: A comparison by substrate and lunar phase of mean number of plankters; bars indicate standerd error bars (n = 15). (a) Cyclopod copepods; (b) Harpacticoid copepods; (c) Ostracods.

Significantly more organisms were found in traps deployed on the full moon than in traps set out on a new moon ($p < 0.01$; Table 2; Table 3; Figure 1c). Both cyclopoid and harpacticoid copepods were more abundant during the full moon than the new moon ($p < 0.05$ and $p < 0.001$, respectively). Ostracod abundances did not change significantly between the two lunar phases.

Substrate Choice

Substrate choice experiments indicated that the demersal plankton taken from sand predominantly resettle in sand ($p \ll 0.001$, Table 4; Figure 3a), while plankton obtained from the rubble reentry traps returned to rubble ($p < 0.05$). Although the individuals from the Pago Bay and Double Reef sand samples made similar choices, the communities were different. In both the sand and coral chambers, the communities from Pago Bay always had a greater proportion of harpacticoids than cyclopoids (Figure 3b). The samples from Double Reef, however, had an approximately equal proportion of cyclopoids to harpacticoids settling in the sand and had a greater proportion of cyclopoids settling in the coral (Figure 3b). Figure 3c shows the proportions of all cyclopoids and harpacticoids in relation to each other.

Table 4: Summary of results for 2-way ANOVAs comparing demersal plankton substrate choice. Data are mean number of plankters per trap followed by the F statistic for the comparison. Numbers in parenthesis are the n for the test.

	Taxa			**Substrate**			**Interaction**
Origin	**Cyc.**	**Ha.**	**F**	**Sand**	**Rub.**	**F**	**F**
Sand (14)	46	384	95.02***	291	138	41.99***	9.95**
Coral Rubble (9)	22	14	6.92*	15	21	5.23*	0.09

* = $p > 0.05$, ** = $p > 0.01$, *** = $p > 0.001$

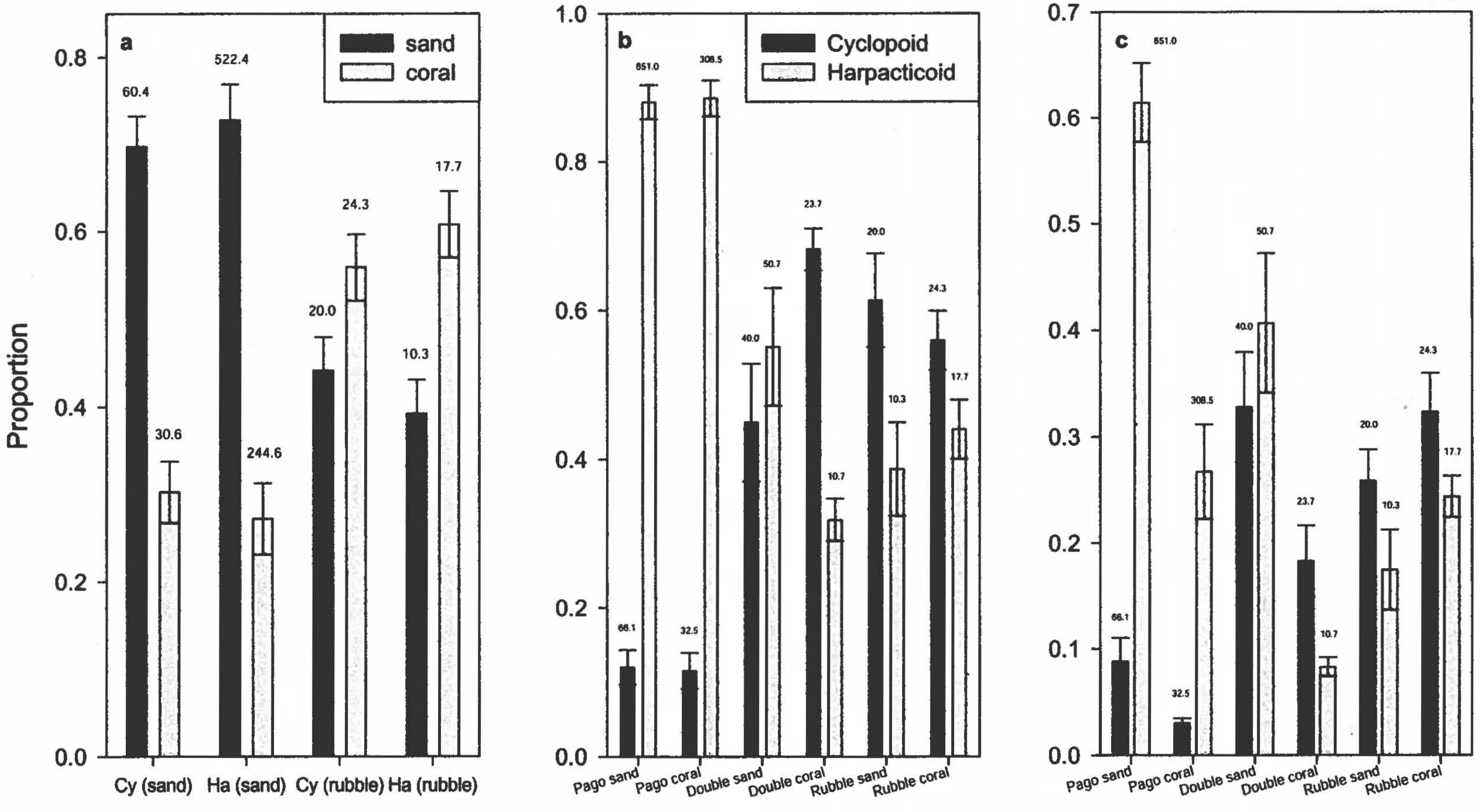

Figure 3: Proportions of cyclopoid and harpacticoid copepods from substrate choice tests. Samples originating from sand and coral rubble are shown separately. Figures (b) and (c) are further divided between samples taken from Pago Bay (n = 11) and Double Reef (n = 3), for sand, and samples obtained from coral rubble filled reentry traps (n=9). (a) proportions of individual taxa between substrates; (b) proportion of cyclopoids and harpacticoids in one substrate; (c) proportions of all cyclopoids and harpacticoids collected from an enclosure. Error bars represent standerd errors. Numbers above bars are the mean number of individuals.

Behavioral Observations

Cyclopoids (Figure 4a) were most active in the water column, with a majority flitting about and another large portion actively swimming (Table 5). No cyclopoids were seen digging into the sand. Harpacticoid copepods (Figure 4b) tended to stay on the bottom. Few were observed swimming or flitting about; most harpacticoids were either crawling on the bottom or digging into the sand. Most ostracods were crawling along the bottom of the dish and on top of the sand, but a few, from specific morphotypes, were always swimming or digging (Figure 4c).

Table 5: Overview of behaviors observed, expressed in percentages and standard errors. Numbers in parenthesis are the mean number of individuals observed. (n=5)

Taxa	Swim	Flit	Crawl	Dig	Motionless
Cyclopoid	21.0 ± 7.0 (5.8)	55.1 ± 5.9 (15.2)	18.1 ± 6.8 (5)	0	5.8 ± 5.5 (1.6)
Harpacticoid	1.3 ± 1.3 (0.2)	12.8 ± 6.1 (2)	71.8 ± 5.2 (11.2)	10.3 ± 4.8 (1.0)	3.8 ± 2.9 (0.6)
Ostracod	3.4 ± 2.2 (0.8)	0.8 ± 0.8 (0.2)	88.1 ± 3.3 (20.8)	7.6 ± 1.4 (1.8)	0

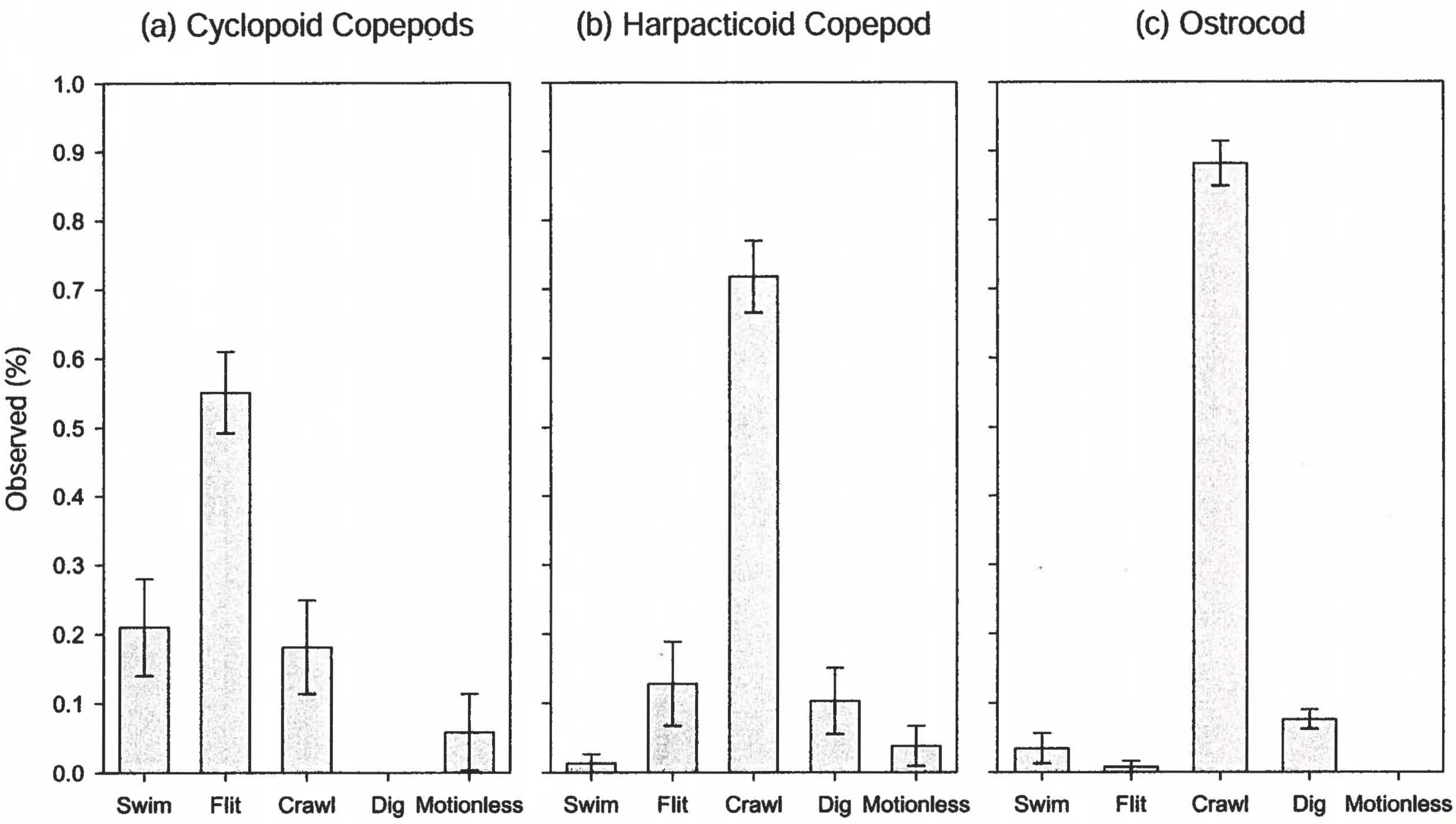

Figure 4: (a-c) Behavior of demersal plankton under observation with standard error bars (n = 5). (a) A majority of the cyclopoid copepods were actively swimming, if not in the water column, at least along the bottom. (b) A majority of the harpacticoid copepods were crawling along the bottom. (c) Most ostracods were crawling along the bottom, although one morphotype also swam and flitted about and another morphotype dug into the bottom.

Sand Entry Test

Harpacticoids took shelter in sand more often, and they were quicker at hiding than cyclopoids (Table 6, Table 7). Cyclopoids and harpacticoids from sand and from the rubble reentry traps differed significantly in the proportion of those that did or did not shelter in the sand ($p < 0.001$). Significant differences in proportions were also seen between the cyclopoids and harpacticoids ($p < 0.001$), between the cyclopoids originating from sand and coral rubble ($p < 0.01$), between the harpacticoids originating from sand and coral rubble ($p < 0.001$), between the cyclopoids and harpacticoids originating from sand ($p < 0.01$), and between cyclopoids and harpacticoids originating from the coral rubble ($p < 0.01$).

Table 6: Substrate entry test results. The ratios of plankters that found shelter in the sand (successful) and those that did not (failed) are given below. Of those plankters that did enter the sand, the average time it took them is given below in seconds and with standard errors.

	Sand Cyclopoid	**Sand Harpacticoid**	**Coral Rubble Cyclopoid**	**Coral Rubble Harpacticoid**
Hid/Visible	11 / 19	28 / 02	02 / 28	11 / 19
Average Time	27 ± 8.4	13 ± 2.5	47 ± 7	24 ± 7.6

Table 7: Results of the *G*-test of independence for the substrate entry tests. Comparisons of origin are between sand and coral rubble and comparisons of taxa are between cyclopoid and harpacticoid copepods. (n = 60, general; n = 30, subcategories)

Comparison	***G* statistic**	**Probability**
Origin, general	22.70964	$p < 0.001$***
Taxa, general	6.661934	$p < 0.01$ ***
Cyclopoid (Origin)	8.070265	$p < 0.01$ **
Harpacticoid (Origin)	17.96117	$p < 0.001$***
Sand (Taxa)	8.823884	$p < 0.01$ **
Coral rubble (Taxa)	2.074003	$p < 0.01$ **

* = $p > 0.05$, ** = $p > 0.01$, *** = $p > 0.001$

DISCUSSION

A comparison between selected taxa collected from the reentry traps at Double Reef and those from other studies (Cahoon *et al.*, 1995; Cahoon and Tronzo, 1988), shows a similar community profile (Figure 5). The taxa examined were amphipods, cyclopoids, harpacticoids, isopods, and ostracods. The similarity in the reentry trap community profiles across the various locations suggests that sand inhabiting demersal plankton communities are globally analogous at the level of class and order (Table 8).

Table 8: R^2 values of multiple regressions of crustacean abundances from multiple studies. Percent abundances of each taxa were regressed against the other four taxa.

Taxa	R^2
Amphipod	0.944
Cyclopoid copepod	0.916
Harpacticoid copepod	0.856
Isopod	0.932
Ostracod	0.664

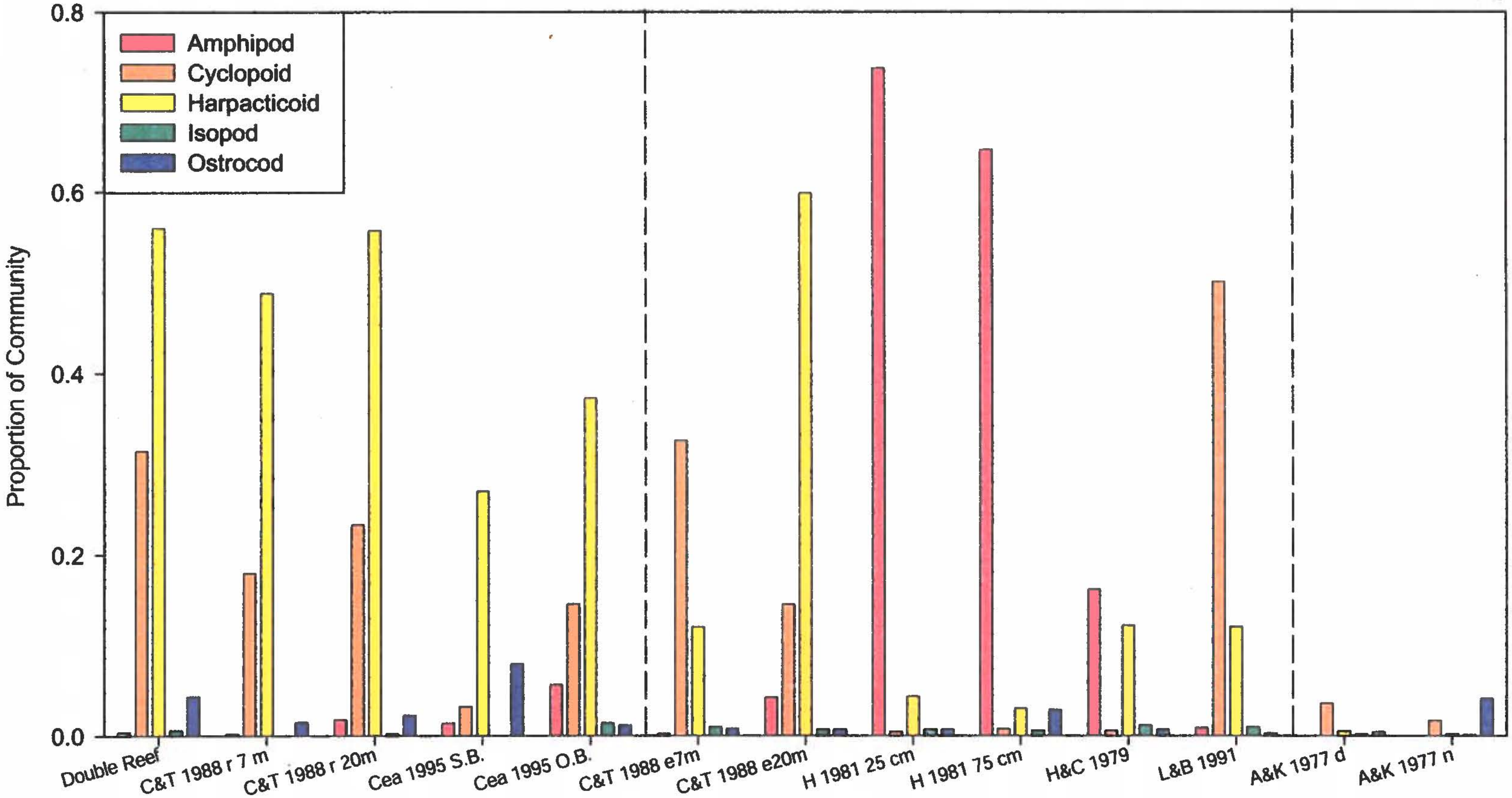

Figure 5: Comparison by seleceted taxa of demersal plankton communities from various studies. Data were taken from this study [Double Reef] (n = 30), from Cahoon and Tronzo (1988), who did their study near Alligator Reef, Upper Matecumbe Key, Florida Keys with both reentry and emergence traps at depths of 7 and 20 meters [C&H 1988 r/e 7/20 m] (n = 6), from Cahoon et al. (1995) with data from Stellwagen Bank, Massachusetts, and Onslow Bay, North Carolina [Cea 1995 S.B./O.B.] (Stellwagen Bank: n = 28; Onslow Bay: n = 141), from Hammer (1981) with data from traps set at 25 and 75 cm near Chalk Cliffs, Santa Catalina Island, California [H 1981 25/75 cm] (n = 18), from Hobson and Chess (1979) with data from Kure and Midway Atolls, Hawaii [H&S 1979] (n = 7), from Lewis and Boers (1991) with data from ~650 m off the west coast of Barbados [L&B, 1991] (n = 149), and from Alldredge and King (1977), who sampled in the Lizard Island lagoon at both day and night [A&K 1977 d/n] (n = 5). The left data set was taken with reentry traps, the middle sets were taken with emergence traps, and the last data set, was taken with plankton tows.

The behavior of the smaller demersal plankton in relation to the lunar phases is likely a result of various functions in their life cycle, rather than as a mechanism to evade predation by planktivorous fish. Demersal cyclopoid and harpacticoid copepods were more abundant in the water column during the full moon when they would be more vulnerable to visual predation. Furthermore, diurnal, planktivorous fish generally prey upon smaller plankters (Hobson and Chess, 1978; Robertson and Howard, 1978), while their nocturnal counterparts target the larger plankters that are generally larger than 2 mm (Alldredge and King, 1980, 1985; Hobson and Chess, 1978). Of the eight species of diurnal planktivores tested, Hobson and Chess (1978) found that the diet of two of the species comprised of only 0.4 % and 0.3 % harpacticoid copepods; harpacticoid copepods were not found in the guts of either the other six diurnal planktivores or the nocturnal planktivores. This evidence suggests that, because of their small size, cyclopoid and harpacticoid copepods are able to venture into the water column with little risk of predation by fish during any of the lunar phases.

The results of this study suggest that demersal plankton are able to determine the type of substrate into which they settle. The field experiments indicated that the cyclopoid and harpacticoid copepods and the ostracods settled primarily in a particular substrate. Cyclopoid copepods and ostracods were more abundant in the coral rubble reentry traps, and the harpacticoid copepods were more abundant in the sand reentry traps. Cyclopoid preference for coral rubble substrate in this study reflects the results of Alldredge and King (1977), who found approximately 2,100 cyclopoids m^{-2} emerging from coral rubble and only 300 to 750 cyclopoids m^{-2} emerging from various grades of sand.

The field results were confirmed by the substrate choice experiments. Whether taken from the sand core or the rubble reentry trap, both the cyclopoids and harpacticoids returned predominantly to their substrate of origin. Thus, it appears that individual plankters can choose the substrate in or upon which they shelter during the day rather than simply settling on whatever substrate is beneath them.

The mechanism by which demersal plankton discriminate between the substrates may be as simple as the ability to make, or find, a hole large enough and deep enough to hide from the light. The difference in abundances of cyclopoids between the substrates is probably caused by the size of interstitial spaces found in the different substrates. The cyclopoids under observation could swim between the spaces of medium-grain sand, which was approximately 0.5 to 1 mm in diameter. Smaller grained sand did not provide large enough interstitial spaces for the cyclopoids to enter. Thus, the largest number of cyclopoids on a reef would find shelter and emerge from the substrate with the largest variety of interstitial space sizes and the greatest number of easily accessible spaces (Alldredge and King, 1977). Of those tested, this substrate would be coral rubble.

In the sand entry tests, the harpacticoids originating from sand burrowed between the grains and many of the cyclopoids were able to shelter in the interstitial spaces. Most of the plankters originating from the rubble reentry traps, however, crawled or swam over the sand; they were generally a different morphotype and too large to shelter in the sand. The few plankters that did hide were either very small, burrowers, or both.

In conclusion, both lunar phase and substrate type influence demersal plankton behavior. In regard to the lunar phase, it is still unclear whether the plankters are reacting to light, tidal currents, or timing, if any of these. The behavior of demersal plankton to different substrate shows a remarkable degree of control during their diel settlement to the bottom. As in the case of parapatric speciation, where a new species evolves within a distinct section of a continuous population, the demersal plankton are a distinct subset of the plankton. Therefore, I propose that a more appropriate name for these organisms is "paraplankton."

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