

Acknowledgments

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A COMPARISON OF DEMERSAL ZOOPLANKTON COLLECTED AT ALLIGATOR REEF, FLORIDA, USING EMERGENCE AND REENTRY TRAPS

Demersal zooplankton have been shown to be important components of a number of marine communities, including coral reefs (Porter and Porter 1977; Alldredge and King 1977), kelp beds (Hammer 1981), and other habitats (Thomas and Jelley 1972). They probably play an important role in the flux of particulate material through benthic communities (Porter and Porter 1977). Demersal zooplankton can also be important prey for fish and other consumers (Alldredge and King 1977, 1980).

Demersal zooplankton are usually sampled by techniques that take advantage of their migration into or out of the plankton. Studies by Alldredge and King (1980, 1985) and Youngbluth (1982) suggest

that sampling methods used to collect demersal zooplankton can have a significant effect on the numbers and kinds of animals collected. The most widely used method to date is emergence trapping, in which zooplankton are collected as they migrate out of the substrate, e.g., Porter and Porter (1977). Another method, reentry trapping, captures zooplankton as they enter the substrate, e.g., Alldredge and King (1980). A primary purpose of this study was to compare results from simultaneous emergence and reentry trapping, and verify Alldredge and King's (1980) finding that reentry traps capture significantly more zooplankton than emergence traps.

Horizontal currents are likely to have major but variable effects on the transport of demersal organisms in the plankton. Organisms migrating high into the water column are likely to be transported laterally to a greater extent than those that remain in the near-bottom layer, as Alldredge and King (1985) have suggested. Thus, the implicit assumption of some other investigators that demersal zooplankton are characteristic residents of a habitat needs qualification. Horizontal transport of migrating demersal zooplankton is probably an important recruitment mechanism and a means by which planktivorous fish associated with reefs and other structures are supported. Demersal zooplankton have been shown to be associated with sand bottoms by Alldredge and King (1977, 1980), so sand bottoms might be an important source of demersal zooplankton for reef communities. Therefore, our purpose in this study was also to assess the abundance of demersal zooplankton on sand bottom habitat. The study addressed the questions: how abundant are different taxa of demersal zooplankton associated with sand bottom habitat? Can different trapping techniques distinguish zooplankters with different propensities for horizontal transport by currents? How do the abundance and taxonomic composition of demersal zooplankton on open carbonate sand compare with the finding of others studying similar sand bottoms?

Materials and Methods

Study sites were located approximately 1.8 km east of Alligator Reef Buoy, ca. 7.5 km southeast of Upper Matecumbe Key in the Florida Keys (lat. 24°41.26'N, long. 80°35.68'W). The sites were characterized by a subtidal, carbonate sand bottom that sloped gently from depths of 2–4 m to depths of over 40 m. Macrophytes occurred sparsely on the bottom

(principally *Thalassia* sp.), with the closest coral structure and associated fish populations several hundred meters downstream. Currents were minimal ($<0.05 \text{ m s}^{-1}$) and flowed to the northeast, parallel to the axis of the Gulf Stream just offshore.

Sampling at the site was conducted with the aid of scuba, supported by the NOAA-National Undersea Research Program's RV *Seahawk*, which operated in the Florida Keys region during March 1985.

Demersal zooplankton were sampled simultaneously by emergence trapping and reentry trapping. The emergence traps were a simplified version of those used by Hobson and Chess (1979), consisting of a single cone of 95 μm mesh netting 1 m high and 21 cm diameter at the mouth (Fig. 1). The mouth of the net was weighted with lead weights sewn into the mouth collar to aid placement on the bottom. A 1 L polyethylene bottle with a polyethylene funnel in the throat was attached to the upper end of the net; the bottles' natural buoyancy extended the traps. Reentry traps were square polyethylene pans, 21 cm per side and 5 cm deep, with removable snap-top lids, approximately one-third filled with defaunated local sand.

Divers deployed six of each type of trap in adjacent groups just after dusk and retrieved them just after dawn on two successive nights in March 1985. Reentry traps were closed and trap bottles from emergence traps capped by divers before return to the surface. The moon was nearly new and rose late each night, thus providing little illumination. The first night's collections were made for 12.75 hours at a depth of 7 m and the second night's for 11.5 hours at a depth of 20 m.

Animals in the collection bottles of the emergence traps were concentrated on a 95 μm mesh sieve, washed into sample bottles, and fixed in a buffered formalin-Rose Bengal solution (ca. 5% formalin final strength). Animals that had entered the reentry traps were washed from the sand with fresh water, causing them to release their grasp on sand grains (R. Higgins¹). The contents of each trap were washed at least 5 times, and until no further animals could be seen in the wash water. All washings were sieved through a 95 μm mesh sieve. The retained material was then poured into sample bottles and fixed as above.

The stained, fixed animals in each sample were examined, identified, and counted with a stereomicroscope. Identifications were made to genus and

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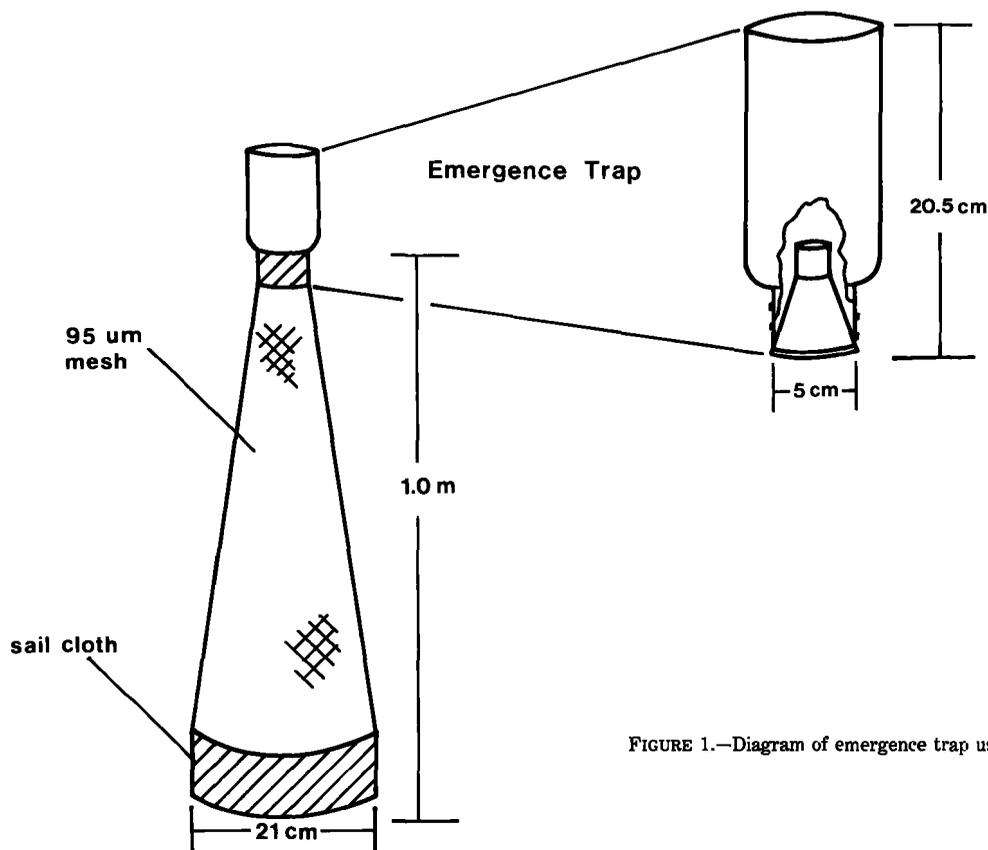


FIGURE 1.—Diagram of emergence trap used in this study.

species when possible; numbers of major taxa and groups are presented here for simplicity and comparative purposes.

Results

The zooplankton caught in the traps at Alligator Reef were dominated by copepods. Other taxa and categories that were collected included chaetognaths, nematodes, ostracods, polychaetes, cumaceans, isopods, amphipods, and mysids, as well as numerous others that were less common or frequently caught (Table 1). Many of these groups, such as the harpacticoid copepods, are well known as benthic or near-bottom forms. Others, such as the calanoid copepods, are known as primarily planktonic animals that are sometimes observed close to the bottom or other substrate. Many larval forms of benthic macroinvertebrates were captured, especially settling stages, such as barnacle cyprids and megalopae.

Comparisons of the total mean numbers of animals caught by each trap type and at each location show that approximately 4 times as many animals were caught by reentry traps as by emergence traps and that about twice as many animals were captured at the 7 m site as at the 20 m site (Table 1). Twelve common groups together accounted for 97.9% of all the animals caught. The results of two-way ANOVAs showed that reentry traps captured significantly more harpacticoid and cyclopoid copepods, ostracods, mysids, polychaetes, and nematodes than emergence traps, while the emergence traps captured significantly more calanoid copepods and isopods (Table 2). Significantly more cumaceans, gammarid amphipods, polychaetes, and nematodes were captured at the 20 m site than at the 7 m site, while significantly more calanoid copepods and chaetognaths were captured at the shallower location (Table 2). The two-way ANOVAs showed significant interaction effects between the trap types and sampling locations on the numbers of harpacticoid and

TABLE 1.—Demersal zooplankton captured in reentry and emergence traps at sand bottom sites (7 m and 20 m) near Alligator Reef, Florida in March 1985. Data are mean numbers of animals m⁻² (SE).

Group	Emergence		Reentry	
	7 m	20 m	7 m	20 m
Harpacticoids ¹	754 (188)	3,040 (726)	16,108 (2,289)	8,866 (845)
Cyclopoids ¹	2,039 (508)	740 (165)	5,943 (1,071)	3,713 (478)
Nematodes ¹	11 (11)	13 (9)	8,840 (1,241)	823 (121)
Calanoids ¹	2,023 (421)	359 (128)	231 (80)	574 (209)
Copepod nauplii ¹	830 (248)	338 (99)	130 (53)	515 (121)
Ostracods ¹	51 (14)	35 (15)	498 (93)	360 (80)
Chaetognaths ¹	289 (47)	17 (8)	357 (70)	126 (65)
Halacarids	4 (4)	0	538 (160)	0
Polychaetes ¹	29 (27)	69 (42)	94 (39)	314 (56)
Caprellid amphipods	0	117 (38)	4 (4)	170 (18)
Gammarid amphipods ¹	11 (5)	100 (49)	54 (19)	119 (32)
Cumaceans ¹	14 (5)	74 (51)	58 (23)	101 (18)
Mysids ¹	7 (5)	39 (8)	72 (27)	43 (18)
Larvaceans	112 (87)	0	29 (29)	11 (11)
Isopods ¹	62 (15)	35 (11)	7 (7)	33 (9)
Lancelets	0	0	14 (7)	69 (9)
Pycnogonids	4 (4)	39 (34)	0	0
Tanaids	0	36 (11)	0	0
Cyphonautes	0	0	0	29 (13)
Penaeids	0	9 (5)	0	18 (7)
Chiton larvae	0	0	11 (7)	7 (5)
Pagurid crabs	0	4 (4)	7 (5)	4 (4)
Cyprids	0	0	11 (7)	0
Hippid crabs	0	0	0	7 (5)
Magelona polychaetes	0	4 (4)	0	0
Fish larvae	0	4 (4)	0	0
Brachyuran crabs	0	4 (4)	0	0
Totals	6,240	5,076	33,006	15,902
Trap totals		11,316		48,908
Site totals: 7 m: 39,250				
20 m: 20,978				
Grand total	60,228			

¹"common" groups caught by both traps at both sites.

TABLE 2.—Results of 2-way ANOVAs comparing effects of sampling location and trap type on numbers of animals caught from 12 common groups. Data are mean/m² and F value for associated comparisons for each category; significantly higher means are underlined. For all comparisons df = 1, 19.

Group	Location			Trap			Interaction
	7 m	20 m	F	Emergence	Reentry	F	F
Harpacticoids	8,431	6,218	2.81	1,793	<u>12,487</u>	65.57**	14.33**
Cyclopoids	3,991	2,361	4.14	1,449	<u>4,828</u>	17.83**	1.17
Nematodes	<u>4,426</u>	454	36.80**	12	<u>4,842</u>	54.20**	41.70**
Calanoids	<u>1,127</u>	476	6.45**	<u>1,267</u>	402	11.39**	14.53**
Copepod nauplii	480	427	3.12	606	305	3.33	4.00
Ostracods	274	207	1.00	43	424	36.30**	1.75
Chaetognaths	<u>323</u>	77	19.51**	165	242	1.88	1.00
Polychaetes	61	<u>203</u>	12.07**	47	<u>204</u>	14.82**	3.69
Gammarid amphipods	32	<u>110</u>	7.26*	51	87	1.00	1.00
Cumaceans	36	<u>89</u>	4.41*	41	79	2.32	2.97
Mysids	40	41	1.00	22	58	4.92*	3.45
Isopods	34	33	1.00	<u>49</u>	20	6.94*	5.41*

* = P < 0.05, ** = P < 0.01.

calanoid copepods, isopods, and nematodes caught (Table 2), indicating that the capture rates of the two trap types varied between locations. Differences in the types and numbers of animals caught by each trap are more important, however.

Reentry traps were much more effective than emergence traps at capturing a greater variety of animals. The most striking differences are the much larger numbers of harpacticoid and cyclopoid copepods captured in reentry traps. In addition to quantitative differences the reentry traps also caught individuals of six groups that were not found in the emergence traps (Table 1). The six groups included the lancelets and five types of demersal larvae.

Conversely, emergence traps were more effective at capturing calanoid copepods and isopods. Specimens of five other taxa were captured only in emergence traps (Table 1).

Analysis of the capture rate of each common group by the two trap types shows significantly different assemblages ($\chi^2 = 881068$, $df = 11$, $P << 0.001$) (Fig. 2a). Furthermore, each trap type caught some relatively rare groups, meaning that the lower capture rate of the emergence traps did not prevent them from capturing groups that did not appear in the reentry traps. Analysis of the capture frequencies of these rarer groups shows that the two trap types capture different assemblages of organisms ($\chi^2 = 25806$, $df = 9$, $P << 0.001$) (Fig. 2b). Therefore, the reentry and emergence traps sampled different fauna or sampled the same fauna differently.

Discussion

Varying migration patterns and swimming behaviors by the various taxa and groups can explain the differences between the assemblages caught by the two trap types. Ascending animals would have to move 1 m off the bottom in order to be captured by the emergence traps. Descending animals would not have been captured at all by the emergence traps, but would only have needed to be a few cm off the bottom to enter the reentry traps. Thus, reentry traps are more likely to capture demersal organisms during their migration than emergence traps if many of these organisms never move very far up into the water column, as Alldredge and King (1985) have shown. Reentry traps also captured settling larvae, which presumably are migrating in only one direction prior to establishing a sessile mode of life. Such larval forms were a small fraction of the total numbers of animals caught, but could be a significant portion of the reentering fauna at times.

Both trap types may have also captured some animals that are holoplanktonic as noted by Robichaux et al. (1981), despite our efforts to prevent this during deployment and recovery of the traps. Some animals may have entered the traps by crawling rather than from the plankton, as Scheibel (1974) observed. Finally, placement of the traps after dusk may have missed animals migrating at or before dusk, but the errors caused by this artifact, as well as errors due to incomplete recovery of animals, are not likely to alter our results significantly.

Another possible explanation for at least some of the differences between capture rates of the two trap types is differential avoidance of one trap type, in this case the emergence traps. Given that emergence traps consist of materials quite unlike those that demersal zooplankton would normally encounter it should not be surprising that they might seek to avoid contact with them. The narrow funnel placed in the mouth of the collection bottles, while necessary to retain animals that have entered the bottle, may exclude others altogether. Some demersal zooplankton, such as calanoid copepods, are well known to exhibit an escape response when placed in contact with surfaces. Reentry traps, on the other hand, work partly by replicating natural sand substrate, reducing the potential for avoidance.

The results show clearly that different sampling techniques yield variable numbers of animals, even within the same taxon, and collect different groups of animals. Thus, evaluation of the demersal zooplankton depends strongly on sampling techniques. Adoption of a single standard sampling technique might appear to be a resolution of the problem, but a standard approach should sample all the organisms that exhibit demersal behavior in a given area, and neither emergence trapping nor reentry trapping does. Furthermore, Stretch (1985) has observed that not all members of a demersal population migrate each night, so trapping techniques that depend on animal migration must consistently underestimate the actual abundance of demersal organisms in association with a given substrate. Tendency to migrate may vary among species, within the life cycle of a given species and from day to day, making accurate sampling of the demersal zooplankton by trapping a logistical impossibility. Collection techniques that directly sample demersal organisms in or on the substrate, such as airlift sampling (Stretch 1985) or sediment coring techniques commonly used to sample meiofauna, should give more accurate abundance estimates, but must be used in conjunction with one or more trapping

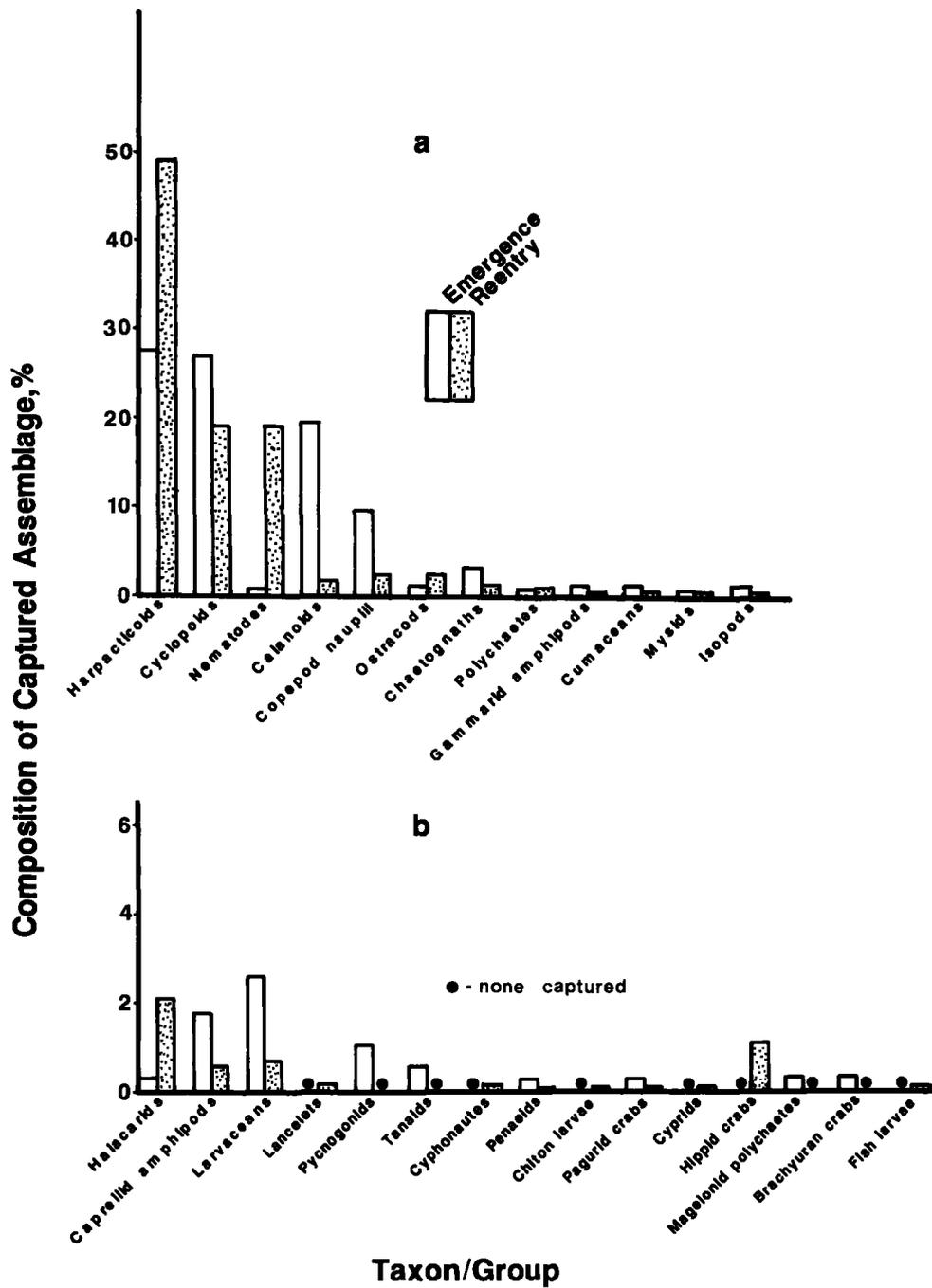


FIGURE 2.—Percentage of the total animals caught by each trap type by taxon or group, in rank order of total abundance, pooled over sites; a) common groups, b) rare groups.

techniques to distinguish migratory from nonmigratory populations.

Comparisons of demersal zooplankton abundances among studies are also made difficult by variation among the trap types and approaches used. Alldredge and King (1980) compared reentry and emergence traps, showing as we have that reentry traps captured very much larger numbers and different proportions of demersal organisms. Aside from studies by Stretch (1985) and ourselves (unpubl. data), we are unaware of any effort to use a direct sampling technique to calibrate a trapping technique. Thus, published abundance estimates for demersal zooplankton abundance are probably low and biased, reflecting the preponderant use of emergence trapping.

Robichaux et al. (1981) pointed out that animals entering traps by crawling can be a significant artifact. Such contamination would probably be a greater problem for reentry traps than for emergence traps. Our reentry traps captured large numbers of nematodes and harpacticoid copepods, which can enter by crawling, but even when they are eliminated altogether from the trap totals, reentry traps still caught twice as many animals as emergence traps (Table 1). Furthermore, at least some nematodes and harpacticoids do swim freely, even if they do not move very far up into the water column, as Alldredge and King (1985) have shown. Thus, we think that reentry trapping reliably yields higher estimates of demersal zooplankton abundance that are more realistic than results from emergence trapping but probably not truly accurate.

Robichaux et al. (1981) also argued that contamination of demersal zooplankton traps by holoplanktonic and crawling organisms causes an overestimate of the actual importance of demersal zooplankton in benthic food webs. We dispute this view on several grounds. First, the emergence trapping technique used by Robichaux et al. (1981), as is the case with others' use of emergence trapping, probably yielded significant underestimates of the actual abundance of demersal zooplankton, as we discuss above. Second, we suspect that all trapping techniques are likely to miss animals that are not migrating actively or that avoid traps, causing further population underestimates. Finally, estimates of demersal zooplankton populations resident within a given habitat may fail to reflect the actual availability of these animals as consumers or prey via transport.

Sand bottom habitats may be important sources of demersal zooplankton for consumers in other

habitats. Currents can carry demersal organisms passively to other habitats. Animals that migrate high into the water column, such as the groups captured especially well by emergence traps, may be carried relatively great distances compared with those that crawl or stay within the near-bottom boundary layer. Furthermore, off-reef foraging by reef dwellers may allow exploitation of demersal organisms on sandy bottoms in the absence of advection. If so, estimates of demersal zooplankton abundance derived from reentry trapping will again be realistic, if not accurate, from the standpoint of community ecology. Therefore, demersal zooplankton are potentially quite important to marine benthic communities, even if the techniques used to sample them are imperfect.

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