

ZOOPLANKTERS THAT EMERGE FROM
THE LAGOON FLOOR AT NIGHT AT
KURE AND MIDWAY ATOLLS, HAWAII

Many zooplankters in nearshore marine habitats are in the water column at night, but spend the daytime sheltered on or near the sea floor (Emery 1968; Glynn 1973; Porter 1974). The diel movements these organisms make between the water column and the sea floor are major features of nearshore ecosystems, and strongly influence many of the fishes in these habitats (Hobson 1968, 1973, 1974, 1975; Hobson and Chess 1976, 1978). Some of these zooplankters are holoplanktonic forms that swarm close to bottom structures by day and disperse above the reef at night. Included are various calanoid copepods (e.g., *Acartia* spp.), cyclopoid copepods (e.g., *Oithona* spp.), mysids (e.g., *Mysidium* spp.), and larval fishes (Emery 1968; Hobson and Chess 1978). Although such forms often occur in caves and other reef openings large enough to accommodate their free-swimming habit, they should be distinguished from the many meroplanktonic forms that by day live in or on the substrate (although this distinction between meroplankton and holoplankton is not always clear-cut).¹ At least some of these neritic holoplankters seem just loosely associated with specific substrata. For example, by day the calanoid *A. tonsa* swarmed close to coral reefs in the tropical Atlantic (Emery 1968) and to kelp forests in the warm temperate eastern Pacific (Hobson and Chess 1976), and also occurred in open waters offshore (Fleminger 1964). The meroplanktonic forms which by day characteristically assume what is essentially a benthonic mode have a much stronger affinity to specific nearshore substrata, and these are the major topic of this paper. Included are various polychaetes, ostracods, copepods, mysids, cumaceans, tanaids, isopods, gammarid amphipods, and various larval forms (Hobson and Chess 1976, 1978, in prep.).

Two recent studies, one on the Barrier Reef (Alldredge and King 1977) and the other in the

Philippine Islands (Porter et al 1977; Porter and Porter 1977), have attempted to quantify the emergence of zooplankters from various coral-reef substrata. These are important papers because they draw attention to what unquestionably is a highly significant and long-neglected aspect of nearshore ecosystems. We suspect, however, that there are problems with these studies. If so, the problems should be promptly recognized because undoubtedly they will spawn similar investigations by other workers elsewhere (e.g., see Randall et al. 1978). Alldredge and King collected their samples in Plexiglas² traps that rested on the bottom and retained organisms that rose into the water column; however, zooplankters from the surrounding water had access to these traps through gaps between the traps' rigid lower edges and irregularities on the sea floor. Earlier (Hobson and Chess 1978), we stated that these collections need to be repeated with this possibility of error eliminated. Obviously, if many zooplankters entered the traps from the surrounding water column, the samples cannot be considered measures of the organisms that emerged from the underlying substrata. The Porter group used traps that were tethered above the sea floor, and so would seem to have offered even greater access to zooplankters from the surrounding water. In fact, the probability that such forms entered the traps seems to us so great that we would have expected that their intent was simply to sample zooplankters near the reef. And yet, in prefacing their findings with statements like (p. 107) "... volumes of plankton produced per m² per hour by different reef substrates during the day and during the night are given in Table 1." they clearly implied that each trap sampled only those organisms that had risen from the substrate directly below it.

Our doubts about these studies, however, were moderated by limitations in our own knowledge of the phenomenon. We had worked extensively with these activity patterns as they relate to fishes (Hobson 1968, 1974; Hobson and Chess 1976, 1978) and had made inferences about the daytime modes of nocturnal zooplankters in nearshore habitats. Still, we had not satisfactorily distin-

¹We define meroplankton as those zooplankters that are in or on the substrate during part of the diel cycle, and holoplankton as those that are in the water column at all hours. As pointed out earlier (Hobson and Chess 1976), these terms have carried different meanings for different authors.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

guished the forms that by day assume essentially a benthonic existence on or in the bottom, from the forms that by day aggregate close to, yet free of, the substrate, or which migrate to deeper water. To increase our understanding of these activities and to acquire a firmer base upon which to assess other studies, we trapped zooplankters that emerged from various substrata in the lagoons of Kure and Midway Atolls, Hawaii during August 1977, making special effort to exclude forms from the surrounding water column.

Methods

Midway and Kure Atolls are about 90 km apart

at the northwestern end of the Hawaiian Archipelago. They are very similar, each having a lagoon that is relatively small (diameter about 8 km) and shallow (maximum depth about 15 m). All our study sites were in approximately 5 to 7 m of water near the outer leeward reefs.

We made seven paired collections, each pair at a different location. One of each pair sampled the organisms that rose from the substrate during the day, and the other sampled the organisms that rose from the same spot during the night. Of the substrates sampled, three were sand (two at Midway, one at Kure), two were a mixture of sand and coral rubble (one at Midway, one at Kure), and two were small heads of both living and dead coral

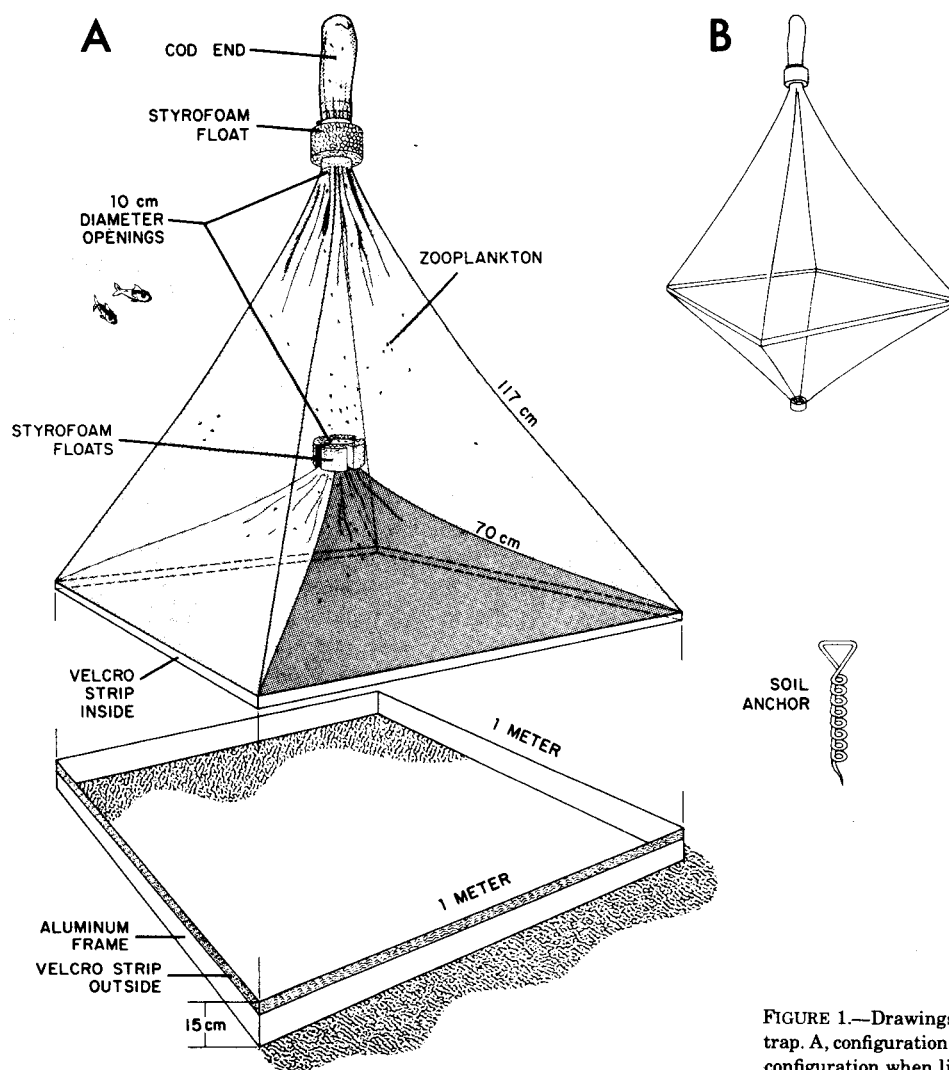


FIGURE 1.—Drawings of the meroplankton trap. A, configuration when set on bottom; B, configuration when lifted by diver.

(about 0.25 to 0.40 m²) surrounded by sand and coral rubble (one at Midway, one at Kure).

It was not our intent to characterize the meroplankton from each substrate—the collections were too few for this; rather, we sought only a general understanding of the types and numbers of organisms that emerge from the lagoon floor.

To begin each set of collections, we placed our trap (Figures 1, 2) in position between sunrise and 0800 h. First we buried the lower portion of the metal frame in the sand and secured it with soil anchors. A tight seal around the base of the trap was judged critical to prevent entry by organisms from the surrounding water. Next we attached the net (which had a 0.333-mm mesh) to this base and allowed it to remain in position throughout the day. We retrieved the net between 1730 h and sunset, washed all materials into the cod end, then removed the materials, and placed them in 10% Formalin. The net, with an empty cod end in place, was then reattached to the frame and left in place

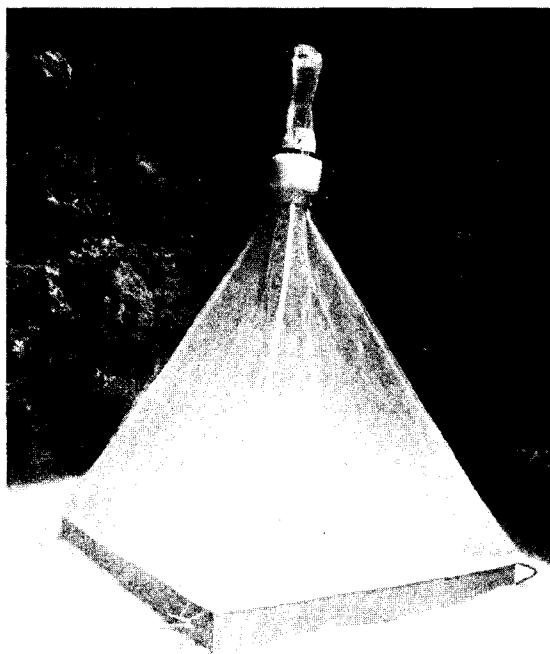


FIGURE 2.—The meroplankton trap in place to sample organisms that emerge from sand in the lagoon of Midway Atoll. If the trap had not been designed to exclude holoplankters, we believe the collections would have included, among other holoplankters, calanoid copepods (*Acartia* sp.) that swarmed close to the adjacent reefs by day, including at their bases, and dispersed throughout the area at night.

throughout the night. The following morning, again between sunrise and 0800, the entire trap—base as well as net—was retrieved, and the collected organisms placed in preservative as before. Having thus completed one set of collections, we moved to another site and repeated the procedure. (We would have reversed the order of collections in some sets, e.g., nighttime first, if appreciable numbers of organisms had been taken by day; as it turned out, however, essentially all organisms were taken in the nighttime samples, as detailed in the Results.)

Our trap worked as follows: Organisms rising from the substrate inside the trap swam upward through the small upper opening of the inner cone and entered the space within the larger outer cone (Figure 1A). Some may have continued up into the cod end, which floated above, but this had no bearing on the collections. When the organisms returned toward the sea floor all except those that happened to descend through the small orifice of the inner cone were trapped where the two cones converged at their common base. In retrieving the net, we reached in under the edge attached to the metal frame and grasped the inner cone around its smaller orifice, thus closing it. We then pulled this out, thus everting the inner cone and producing a diamond-shaped bag (Figure 1B) with the orifice closed in our grasp at one end and the cod end at the other. We then towed the net back to the boat, still enclosing the smaller orifice in our grasp, so that, as we swam, all materials inside were swept back into the trailing cod end.

Results

The organisms collected by our trap, day and night, are listed in Table 1. The general absence of organisms in the daytime collections was predictable, based on the many reports which have concluded that the diel emergence of such forms is primarily a nocturnal phenomenon (see references listed above). Among organisms we observed swarming close to reef structures in the vicinity of our trap during the day were calanoid copepods (most of them *Acartia* sp.), mysids, and larval fishes. Although such forms disperse in the water column at night (Emery 1968; Hobson and Chess 1976, 1978), their absence from our trap collections is consistent with the contention that the holoplanktonic forms associated in varying degree with the reef are distinct from those organisms that live by day in or on the substrate.

TABLE 1.—Organisms trapped by day and night at Kure and Midway Atolls.

Zooplankton category	Day (n = 7)		Night (n = 7)	
	Percent occurrence	Mean no. individuals	Percent occurrence	Mean no. individuals
Foraminiferans ¹	43	2.9	100	18.9
Polychaetes ²	29	0.5	100	7.3
Gastropods ³	57	0.1	100	7.0
Ostracods ⁴	0	0.0	86	1.7
Calanoid copepods ⁵	0	0.0	100	17.7
Cyclopoid copepods	0	0.0	43	1.4
Harpacticoid copepods ⁶	0	0.0	100	31.0
Mysids	0	0.0	14	0.1
Cumaceans	0	0.0	29	0.6
Tanaids ⁷	0	0.0	86	11.9
Isopods ⁸	0	0.0	71	3.0
Cirripedian larvae	0	0.0	29	0.6
Gammarid amphipods ⁹	0	0.0	100	40.1
Caprellid amphipods	0	0.0	43	1.0
Caridean larvae	0	0.0	43	60.9
Candean adults and juveniles	0	0.0	86	18.4
Reptantian zoea	0	0.0	57	17.0
Brachyuran megalops	0	0.0	71	6.3
Anomuran glaucothoe	0	0.0	43	1.3
Chaetognaths ¹⁰	0	0.0	57	5.9
Ascidian larvae	0	0.0	14	1.0

¹All foraminiferans were either *Tretomphalus* sp. (72%) or *Amphistigina* sp. (28%).

²The major polychaete was *Polyophthalmus* sp.

³Included one 8-mm dorid opisthobranch; the rest were prosobranchs <3 mm long.

⁴The major ostracod was a species of *Cylindroleberinae*.

⁵All identifiable calanoids were *Paramisophria* sp., probably undescribed (Abraham Fleminger, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. April 1978).

⁶All identified harpacticoids were of a species of the family Peltidiidae.

⁷All the tanaids appeared to be of a species of *Leptochelia*, close to *L. dubia* (see Hobson and Chess 1976).

⁸Major isopods were: *Cirolana* sp., *Ianiropsis* sp., *Munna* sp., anthurids, and cryptoniscid larvae.

⁹Gammarids included: *Aoroides* sp., *Dexaminoides orientalis*, *Lilgeborgia* sp., a eusiid, an oedicerotid, and a phoxocephalid.

¹⁰All chaetognaths were *Spadella gaelanoi* (A. Alvarino, Fishery Biologist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, pers. commun. Sept. 1978).

Discussion

Our collections and collecting sites were too few to comprehensively quantify the zooplankters that emerge from the lagoon substrata at Kure and Midway Atolls. Despite its limitations, however, this study increases our understanding of the kinds of organisms that have this habit. Furthermore, it indicates there may be serious problems with the more extensive studies of Alldredge and King (1977), Porter et al. (1977), and Porter and Porter (1977).

Certainly some of the differences between their samples and ours are unrelated to sampling problems. We assume, e.g., that the zooplankton fauna at Kure and Midway Atolls is distinguishable from the zooplankton fauna in the more tropical latitudes of the western Pacific Ocean where the Alldredge and Porter groups studied. It is unlikely, however, that zoogeographic variations can account for certain of the more striking differences

between their samples and ours. The predominant forms in their collections were calanoid and cyclopoid copepods. Alldredge and King (1977) calculated that during the night a mean of 6,679 calanoids emerged from each square meter of the reef face, and Porter et al. (1977) reported that over 10,000 calanoids emerged during the night from each square meter of branching coral in their study area. In comparison, our night-long collections from a variety of substrata, including coral, yielded a mean of only 17.7 calanoids/m². Of course, we did not sample a well-developed reef. Only two of our sites included living coral, and these were isolated heads (our traps required a bed of sand). So habitat features could have contributed differences between the collections. Nevertheless, if one considers the species of calanoids and cyclopoids collected by Alldredge and King, there are strong indications that the large numbers reported were inflated by holoplanktonic forms. The only calanoids and cyclopoids they identified were *Acartia* spp. and *Oncaea* spp. Species of these two genera are exceedingly numerous in the water column during both day and night (see Emery 1968; Hobson and Chess 1976), and we question whether they could in fact assume a benthonic mode. As stated (Hobson and Chess 1978:149) "We would expect organisms that live in the substrate by day to have morphological features reflecting this habit that distinguish them from holoplanktonic relatives at the generic level or higher." Although the Porter group did not identify their calanoids and cyclopoids to lower taxa, they too sampled western Pacific reefs and so the copepods that similarly dominated their collections may well have been the same, or very similar, to those taken by Alldredge and King. All our calanoids, on the other hand, appeared to be referable to the little known genus *Paramisophria* (Abraham Fleminger, Associate Research Biologist, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. April 1978). This fact agrees with our contention that zooplankters which periodically enter the substrate should be morphologically distinctive. If the diurnal benthic mode of this species is a generic characteristic, which seems probable, then its poorly known status likely stems from failure to be sampled by standard plankton-collecting techniques.

During a marine survey of the Palau Islands, Randall et al. (1978) attempted to measure the zooplankters that emerged from the sea floor using traps "... built according to the design of Porter

and Porter (1977).” Their samples, taken above coral and sand substrata, included far fewer copepods than the Alldredge and Porter collections (but many more than ours); nevertheless, they recognized the presence of holoplanktonic forms (e.g., siphonophores, crustacean and fish eggs, and fish larvae), which they assumed “. . . either swam (or were carried) under the base of the trap from the open water . . .”

So we believe that the studies by the Alldredge and Porter groups are flawed by the unrecognized occurrence in their samples of organisms from the surrounding water column. At Enewetak Atoll (Hobson and Chess 1978), we concluded that many of the zooplankters above lagoon reefs at night are visitors from the deeper water. If this circumstance existed where Alldredge and Porter set their traps, then their collections probably included deep-water forms. If so, the figures presented as measures of zooplankters that emerge from defined areas of particular nearshore substrata probably include not only holoplankters associated by day with other nearshore substrata but also holoplankters from outside the nearshore realm.

We consider our collections conservative estimates of the numbers of organisms that emerge from the sampled substrata. It may be that some forms which ordinarily rise into the water column were inhibited by our trap, and undoubtedly some that rose into the trap found their way back to the sea floor. But we feel our trap should have been as effective in capturing emerging zooplankters as those used by the Alldredge and Porter groups. Possibly some strictly benthic forms entered our samples by climbing up the inside of the trap. The few prosobranch gastropods that were taken may have been trapped this way, although they were small enough to have been swept up into the water column by surge, or perhaps to possess some flotation device that periodically permits a planktonic mode, as is the case with certain foraminiferans (e.g., *Tretomphalus* and perhaps *Amphistigina*). Significantly, most of the organisms collected belong to groups that include forms we have collected in the water column at night elsewhere: e.g., the foraminiferan genus *Tretomphalus* (at Majuro and Enewetak Atolls: Hobson and Chess 1973, 1976); the polychaete genus *Polyophthalmus* (at Enewetak Atoll: Hobson and Chess 1978); and the ostracod subfamily *Cylindroleberdinae*, the tanaid genus *Leptochelia*, the isopod genera *Cirolana* and *Munna*, and family Anthuridae, the

gammarid genus *Aoroides*, and families Eusiridae, Oedicerotidae, and Phoxocephalidae (at Santa Catalina, southern California: Hobson and Chess 1976, in prep). The forms that predominated in our collections belong to groups that were only relatively minor elements in the Alldredge and Porter collections. Most, in fact, were lumped by Porter et al. (1977) in their summarizing Figure 2 as “miscellaneous.” This is not because they took fewer of these forms than we did, but rather because copepods and larvaceans so dominated their collections.

We believe that the major difference between our collections and those of the Alldredge and Porter groups is that we excluded organisms from the surrounding water column. Alldredge and King (1977) were aware that outside organisms could enter through the gaps around the base of their traps, but seemed more concerned about organisms inside that might have escaped. They dismissed both possibilities as significant sources of error with the statement (p. 318) “. . . as many plankters may also enter the trap through these gaps as escape through them.” But because these devices were, after all, traps, probably many more zooplankters came in than went out. And if in fact zooplankters entered the traps through these gaps, it seems certain that forms from the surrounding water, including holoplankters, were continuously captured. Porter et al. (1977) reported about 1.5 to 2 times as many zooplankters as did Alldredge and King. They attributed this difference to more effective methods and equipment, but their traps, tethered above the reef, may simply have been more readily entered by holoplankters. This would also account for the relatively large numbers of zooplankters they trapped by day. Both studies may have suffered from a misconception about the movements of these organisms. Alldredge and King doubted that many escaped through the gaps around the bases of their traps because they assumed (p. 318) “. . . emerging plankton swim primarily upward . . .” The Porter group would seem to have based their trap design—inverted cones tethered above the bottom—on the same assumption. But while these animals certainly rise progressively higher in the water column after emerging from the sea floor, generally they swim—some flit—in short, irregular tangents more horizontal than vertical (based on our direct observations of a wide variety of forms in many locations). In any event if holoplankton did enter these traps in significant numbers, then

the samples taken should not be presented as measurements of the forms that emerged from the underlying substrata.

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