

MESOPELAGIC MICRONEKTON IN HAWAIIAN WATERS: FAUNAL COMPOSITION, STANDING STOCK, AND DIEL VERTICAL MIGRATION

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ABSTRACT

On one cruise off leeward Oahu, Hawaii, micronekton from 9 deep-oblique mid-water trawl tows (0-1,200 m) and a 24-h series of 14 consecutive shallow-oblique tows (0-400 m) were sorted into 16 faunal groups, enumerated, and weighed. Diel-related trawl avoidance was not significant in deep tows. Mean total micronekton standing stocks for the deep tows were 898 organisms/100 m² ocean surface and 494 g (wet weight)/100 m² ocean surface. Fishes comprised half of the total numbers and biomass, while crustaceans contributed one-third of the total numbers and one-fifth of the biomass. Of the micronekton deeper than 400 m during the day, 43% of the number of organisms with 47% of the biomass migrated into the upper 400 m at night.

Micronekton play important roles in the oceanic ecosystem, yet few studies have examined the whole fauna in one area to measure standing stock, percent standing stock involved in diel vertical migration, or the relative contributions of major groups to the standing stock. This study considers such data taken on one cruise off Hawaii in the fall of 1972.

Samples were taken over 2,500-m deep waters 10-25 km off the leeward (west) coast of Oahu, in the Hawaiian Archipelago (approximately between lat. 21°15'N, long. 158°15'W and lat. 21°30'N, long. 158°22'W). Physical, chemical, and microbiological data are available for the sampling area (Schuert 1970; Gundersen et al. 1972) and nearby Station Gollum (lat. 22°10'N, long. 158°00'W) (Gordon 1970, 1971). A broad thermocline about 50-500 m deep is present throughout the year (Figure 1). A salinity minimum of 34.0‰ occurs at 400-500 m and a maximum of about 35.2‰ occurs around 100 m (Gordon 1970). The oxygen concentration varies from a minimum of 0.7 ml O₂/liter at 600-800 m to a maximum of about 5.3 ml O₂/liter at the surface (Gordon 1970). Water transparency is very high. In August 1972, noon irradiance measurements at a nearby station, lat. 28°29'N, long. 155°14'W, dropped from a surface level of $7 \times 10^2 \mu\text{W}/\text{cm}^2$ (at 471 nm) to 1.8×10^{-3}

$\mu\text{W}/\text{cm}^2$) at 471 nm) 400 m deep, $k = 0.029$ below 200 m (E. M. Kampa, pers. commun.) (cf. G. L. Clarke 1971:43). Primary productivity in this area has been estimated at 50 g C/m²·yr (S. A. Cattell, pers. commun.). The mean seasonal standing stock of zooplankton in the upper 200-m layer off Oahu is about 2.6 g (wet weight)/m² (Nakamura 1967).

GEAR AND METHODS

Trawl

All samples were taken with a 10-foot (3-m) Isaacs-Kidd Mid-water Trawl (IKMT) of standard design (Devereaux and Winsett 1953). The anterior portion of the net was lined with 6.35-mm (stretch) knotless nylon mesh; the middle portion was lined with 4.75-mm knotless nylon mesh; and the cod end was a 1.0-m diameter plankton net of 0.333-mm Nitex² mesh. Water flow was measured with a flowmeter (General Oceanics 2030) suspended near the center of the mouth, about 1 m inside the net. A time-depth recorder (TDR) (Benthos 1170-1000 or -2500) provided data on the sampling path.

Trawling Method

All samples were taken on cruise TEUTHIS-18

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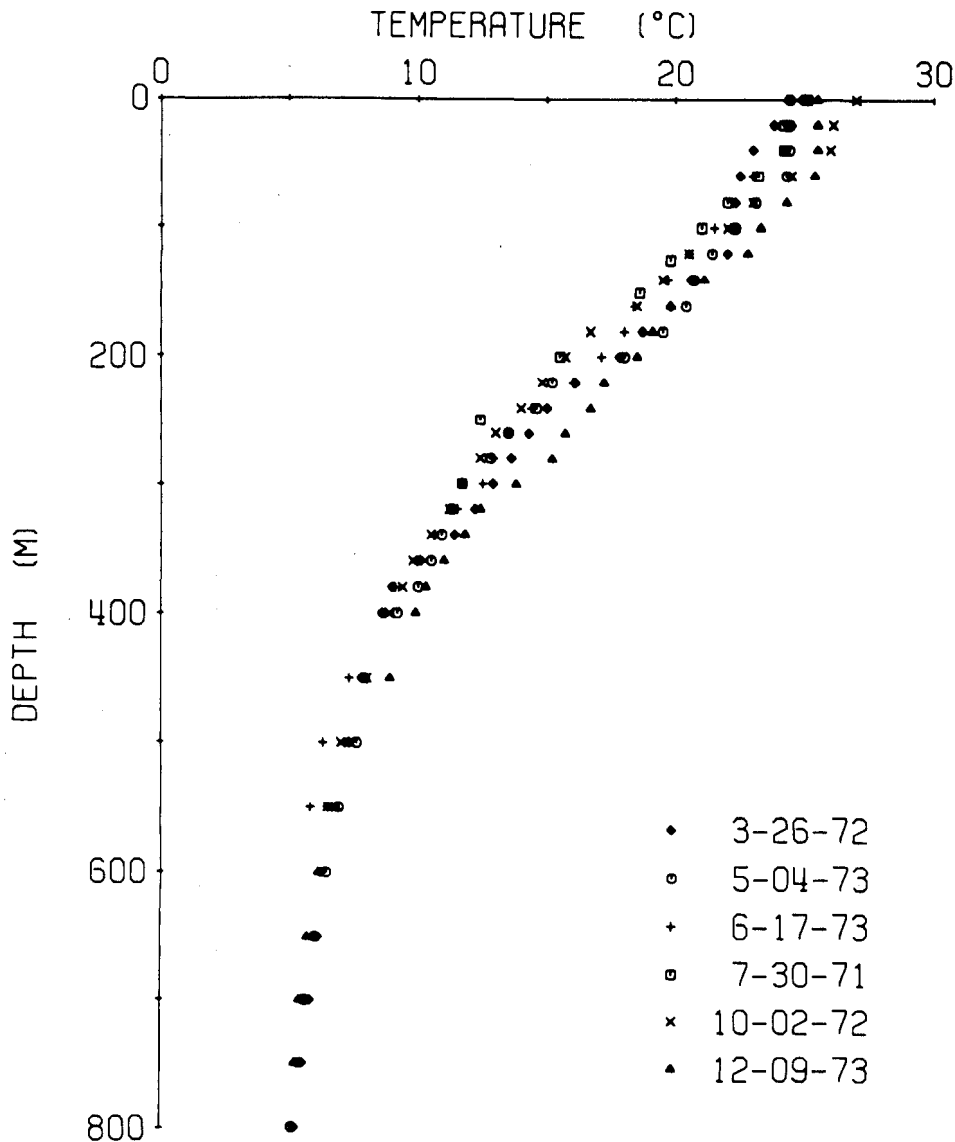


FIGURE 1.—Temperature-depth profiles taken by expendable bathythermographs in the sampling area.

on the University of Hawaii RV *Teritu*, 29 September to 3 October 1972 (Table 1). Sunrise occurred at about 0630 h, sunset at 1830. The moon was in its last quarter; on the last day of the cruise it rose at 0330 and set at about 1530.

All hauls were oblique and sampled primarily during descent. Two types of tows were made: deep tows 0-ca. 1,200 m (Figure 2a) and shallow tows 0-ca. 400 m (Figure 2b). Two deep-tow series (four day tows, five night tows total) were separated by a 24-h shallow-tow series (six day

tows, six night tows); three twilight tows (no. 180, 184, 197) were also made, but the data were not included in computations of mean standing stocks. The two types of tows were designed to complement each other and provide data on diel vertical migrations; the two deep series were intended to examine day-to-day catch variability. The sampling depths were based on the results of previous horizontal sampling which indicated that nearly all micronekton resided between 400 and 1,200 m during the day.

TABLE 1.—Tow data for TEUTHIS-18.

Tow number	Date	Local time		Number flowmeter revolutions	Max. depth (m)
		Begin	End		
180	9/29	1703	2025	517,814	1,350
181		2040	0213	998,460	1,500
182	9/30	0235	0408	290,325	365
183		0657	1203	1,061,855	1,160
184		1221	1710	841,941	1,250
185		1912	0002	884,407	1,320
186	10/1	0015	0500	872,342	1,350
187		0522	0657	399,056	390
188		0716	0851	307,434	400
189		0904	1040	336,306	400
190		1051	1220	284,953	400
191		1236	1408	346,136	500
192		1429	1607	307,172	405
193		1620	1751	306,759	410
194		1758	1928	275,434	400
195		1937	2110	295,355	400
196		2117	2250	284,199	395
197		2257	0029	293,163	440
198	10/2	0036	0210	274,276	415
199		0232	0409	308,441	420
200		0421	0554	305,249	400
201		0630	1117	935,456	1,200
202		1134	1612	844,093	1,240
203		1856	2330	857,374	1,310
204		2340	0434	935,631	1,210

the trawl was retrieved as fast as possible. Total duration of shallow tows was about 1.5 h, that of the retrieval phase about 0.3 h. For deep tows, the first 1,100 m of cable were let out in the same manner as for the shallow tows. Beyond 1,100 m, 200 m of cable were let out at 50 m/min every 10 min until 3,400 m of cable were out. After 10 min at this depth (about 1,200 m), the trawl was retrieved as fast as possible. Total duration of deep tows was about 5 h; retrieval took about 1 h. The distribution of mean sampling times in each 100-m depth interval is shown in Table 2. By inspection, the variability seemed small enough to treat all tows within each type equally.

TABLE 2.—Distribution of mean sampling time per tow (minutes) and standard deviation (SD) with depth.

Sample depth interval (m)	Shallow				Deep			
	Day (6 tows)		Night (7 tows)		Day (4 tows)		Night (5 tows)	
	Mean time/tow (min)	SD	Mean time/tow (min)	SD	Mean time/tow (min)	SD	Mean time/tow (min)	SD
0-100	21.0	0.0	21.3	1.4	19.3	4.9	17.4	3.2
101-200	22.0	1.4	21.3	1.0	20.3	6.7	17.8	2.8
201-300	21.5	1.7	22.2	2.4	24.3	0.6	21.4	3.9
301-400	26.0	1.4	25.2	3.1	26.0	4.6	28.4	3.8
> 400	3.5	0.5	2.7	4.6				
0-400	94.7	2.7	92.9	2.3	90.0	7.9	89.0	4.5
401-500					24.7	3.1	25.0	2.1
501-600					24.7	11.6	18.8	4.4
601-700					23.0	1.7	29.6	4.4
701-800					22.3	2.8	21.8	2.7
801-900					39.7	7.1	34.0	5.6
901-1,000					23.7	7.8	20.6	5.6
1,001-1,100					17.7	8.6	14.8	2.4
1,101-1,200					19.7	14.4	13.4	3.5
1,201-1,300					10.7	9.7	11.0	2.0
1,301-1,400					0.0		10.6	7.2
1,401-1,500					0.0		7.4	16.6
Total					291.0	13.7	292.0	23.3

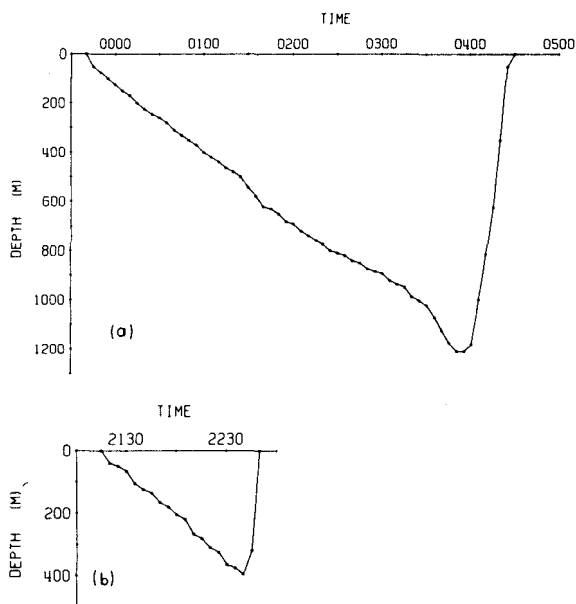


FIGURE 2.—Time-depth records for typical tows, depth plotted every 5 min. a. Deep tow, no. 204. b. Shallow tow, no. 196.

A stepped sampling strategy was adopted. The ship speed was 100 m/min (3.5 knots) for all sampling except during retrieval when the ship was nearly stopped. For the shallow tows, 100 m of cable were let out at 50 m/min every 5 min until 1,100 m of cable were out. This placed the trawl at about the 400-m depth. After 5 min at this depth,

Sample Processing

For this study, micronekton was defined as the pelagic marine animals longer than 1 cm caught by the 10-foot IKMT with the trawling methods described above. Each catch was preserved in buffered 7% seawater-Formalin. The animals were originally sorted to family or genus but subsequently were lumped into larger groups chosen to roughly discriminate between vertical migrators and non-migrators, as well as among trophic groups (Table 3). Group names are capitalized in the text. All micronekton except siphonophores were counted, and all groups were weighed (blotted wet weight ± 0.01 g). Siphonophore biomass was included in the Cnidaria group, but the

TABLE 3.—Group composition used to sort each catch.

1. Myctophidae.
2. <i>Cyclothone</i> (Gonostomatidae).
3. Other Gonostomatidae.
4. Sternoptychidae.
5. Other Stomiatoidei: Astronesthidae, Chauliodontidae, Idianthidae, Malacosteidae, Melanostomiidae, Stomiidae.
6. Anguilliformes: Cyemidae, Eurypharyngidae, Leptocephali, Nemichthyidae, Serrivomeridae.
7. Miscellaneous fishes: Alepisauridae, Apogonidae, Bathylagidae, Bregmaceroiidae, Brotulidae, Ceratioidei, Cetomimidae, Chiasmodontidae, Evermannellidae, Giganturidae, Macrouridae, Melamphaeidae, Neoscopelidae, Omosudidae, Opisthoproctidae, Paralepididae, Scorpaenidae, Trachipteridae, Zeidae, Zoarcidae, larval neritic, unidentified larval mid-water.
8. Caridea: Ophiorhidae, Pandalidae, Pasaphaeidae.
9. Penaeidae: Penaeidae, Sergestidae.
10. Euphausiacea: Benth euphausiidae, Euphausiidae.
11. Mysidacea: Eucoppeidae, Lophogastridae.
12. Miscellaneous Crustacea: Amphipoda, Isopoda, Ostracoda.
13. Cephalopoda.
14. Tunicata: Pyrosomidae, Salpidae.
15. Cnidaria: Hydrozoa, Scyphozoa, Siphonophora.
16. Miscellaneous invertebrates: Annelida, Ctenophora, Heteropoda, Pteropoda, Nemertea.
17. Zooplankton: Copepoda, larval Stomatopoda, other meroplankton, organisms ≤ 1 cm, residue.
Pooled classifications
Total fishes = Groups 1-7.
Total Crustacea = Groups 8-12.
Other invertebrates = Groups 14-16.
Total micronekton = Groups 1-16.

number of siphonophores could not be determined from the assorted zooids (Pugh 1974), and the numerical standing stock of Cnidaria is thus slightly underestimated. Organisms larger than 10 g/individual were weighed separately, but their weights and abundance were included in group totals. Most animals with greatest linear dimensions of about 1 cm or less, such as the euphausiid *Stylocheiron* spp., were placed into the zooplankton group although some sergestids in this size range were included in Penaeidea. Standing stocks of zooplankton shrimps were calculated from subsamples (Folsom splitter) of one deep tow.

Calculations

The volume of water filtered by each tow was determined by multiplying the distance travelled (as determined by the flowmeter) by the area of the net mouth. Mouth areas from 7.08 to 8.19 m² have been reported for the 10-foot IKMT (Brooks et al. 1974). We used 7.7 m² for our trawl. Zooplankton biomass was calculated for a mouth area of 7.7 m², the full IKMT mouth, and 0.785 m², the area of the cod end mouth. The true zooplankton concentration probably lies somewhere between these values because the anterior por-

tions of the trawl funnel some zooplankton into the cod end while others pass through the meshes (Banse and Semon 1963; Hopkins 1966; Friedl 1971).

To calculate the number of organisms or biomass of each group per 100 m² of ocean surface, the catch was divided by the volume of water filtered; this quotient was multiplied by the maximum depth of the tow and the product was then multiplied by 100. This computation assumes all depths were sampled equally.

RESULTS

Standing Stock

The standing stocks from deep-day and deep-night tows were not significantly different (*t*-test, $P < 0.05$) in either number of organisms or biomass for most groups, including total micronekton. Only the numbers of miscellaneous fishes and Mysidacea showed significant diel differences. Likewise there were no significant differences ($P < 0.05$) between the two series of deep tows (tows 183-186 vs. 201-204). Consequently we treated all deep tows as replicates and pooled the data to compute mean micronekton standing stocks for the 0- to 1,200-m deep water column (Tables 4, 5). Shallow-day (tows 188-193) and shallow-night (tows 182, 195-200) data were obviously different and were treated separately in these tables. The percentage composition of the fauna by group is illustrated in Figure 3 for each of the three classes of tows.

The mean standing stocks of total micronekton for the 0- to 1,200-m water column are about 900 organisms and 500 g wet weight/100 m² of ocean surface (Tables 4, 5). Fishes comprised over one-half of both the total numbers and biomass; crustaceans constituted about one-third of the numbers and one-fifth of the biomass, while the cephalopods contributed only one-hundredth of the numbers but one-tenth of the biomass (Tables 4, 5). *Cyclothone* were more than twice as numerous as any of the other 15 groups, totalling almost 35% of the individuals caught (Figure 3a). The distribution of biomass among the groups varied less than the distribution of the abundance. No group contributed more than the Myctophidae which comprised 13% of total biomass (Figure 3a). A comparison of group rank by biomass with rank by abundance indicates that most of the more

TABLE 4.—Micronekton standing stock, mean number of organisms per 100 m² ocean surface. Standard deviation in parentheses.

Group	Day		Night	
	0-1,200 m	0-400 m	0-400 m	0-400 m
Myctophidae	108.13 (45.71)	1.02 (1.15)	80.72 (22.65)	
Cyclothone	308.29 (103.34)	6.07 (8.84)	19.48 (39.01)	
Other				
Gonostomatidae	25.77 (3.70)	3.25 (3.84)	22.13 (8.56)	
Sternoptychidae	22.97 (5.98)	0.42 (0.78)	4.36 (1.47)	
Other Stomiatoidei	3.92 (2.04)	0.00	2.68 (1.70)	
Anguilliformes	11.43 (4.46)	2.64 (1.04)	2.96 (2.23)	
Misc. fishes	27.49 (7.64)	16.31 (5.68)	21.08 (5.83)	
Caridea	40.18 (5.93)	1.70 (2.21)	27.52 (11.18)	
Penaeidea	137.90 (34.99)	6.83 (3.74)	132.90 (21.69)	
Euphausiacea	97.79 (28.16)	6.79 (5.77)	69.01 (11.50)	
Mysidacea	9.89 (3.02)	0.00	8.73 (6.67)	
Misc. Crustacea	4.08 (6.72)	0.00	1.88 (1.54)	
Cephalopoda	8.44 (2.04)	3.60 (1.98)	5.95 (1.81)	
Tunicata	28.05 (14.10)	50.26 (24.73)	25.01 (10.97)	
Cnidaria	10.80 (9.41)	11.82 (2.49)	11.47 (8.81)	
Misc. invertebrates	52.93 (25.02)	55.55 (7.73)	42.04 (10.03)	
Total micronekton	898.07 (149.50)	166.27 (16.45)	477.94 (69.27)	
Total fishes	508.00 (133.50)	29.71 (7.48)	153.41 (60.43)	
Total Crustacea	289.84 (54.25)	15.32 (4.92)	240.04 (13.91)	
Cephalopoda	8.44 (2.04)	3.60 (1.98)	5.95 (1.81)	
Other invertebrates	91.78 (25.22)	117.63 (19.26)	78.52 (22.71)	
No. organisms caught	12,037	1,576	5,136	
No. tows	9	6	7	

TABLE 5.—Micronekton standing stock, mean biomass, grams wet weight per 100 m² ocean surface. Standard deviation in parentheses.

Group	Day		Night	
	0-1,200 m	0-400 m	0-400 m	0-400 m
Myctophidae	65.71 (20.36)	0.19 (0.17)	69.85 (12.26)	
Cyclothone	45.91 (11.26)	0.46 (0.75)	1.20 (2.92)	
Other				
Gonostomatidae	14.92 (8.48)	0.41 (0.49)	29.24 (25.22)	
Sternoptychidae	25.05 (14.02)	0.39 (0.91)	7.45 (2.75)	
Other Stomiatoidei	15.56 (12.53)	0.00	13.36 (14.73)	
Anguilliformes	48.18 (43.65)	2.40 (3.04)	1.53 (1.63)	
Misc. fishes	41.37 (40.16)	2.65 (0.93)	9.46 (6.35)	
Caridea	50.49 (21.07)	0.15 (0.28)	30.27 (13.11)	
Penaeidea	31.59 (10.61)	0.13 (0.10)	22.71 (3.88)	
Euphausiacea	18.52 (3.98)	0.86 (0.80)	12.28 (1.57)	
Mysidacea	8.80 (9.76)	0.00	4.42 (3.45)	
Misc. Crustacea	1.09 (1.92)	0.00	1.09 (0.78)	
Cephalopoda	48.71 (47.46)	2.02 (2.02)	13.84 (16.28)	
Tunicata	34.07 (42.52)	5.90 (3.50)	21.68 (15.00)	
Cnidaria	40.86 (46.86)	10.50 (5.50)	11.34 (12.87)	
Misc. invertebrates	3.38 (3.49)	6.61 (2.35)	1.39 (0.33)	
Total micronekton	494.20 (99.30)	32.68 (6.58)	251.11 (53.46)	
Total fishes	256.70 (81.30)	6.50 (2.99)	132.09 (39.33)	
Total Crustacea	110.49 (36.15)	1.14 (1.06)	70.77 (12.30)	
Cephalopoda	48.71 (47.46)	2.02 (2.02)	13.84 (16.28)	
Other invertebrates	78.31 (53.50)	23.01 (8.34)	34.41 (21.93)	
Zooplankton ¹	48.12 (21.64)	15.24 (4.07)	49.20 (12.30)	
Zooplankton ²	471.95 (212.26)	149.45 (39.94)	482.57 (120.91)	

¹Calculated assuming 7.7 m² net mouth, full 10-foot IKMT mouth.
²Calculated assuming 0.785 m² net mouth, cod end mouth area.

abundant groups are comprised of small individuals (Figure 3a). Biomass estimates for zooplankton in deep tows ranged from about 10 to 100% of the total micronekton, depending on which mouth area was used for calculation (Table 5).

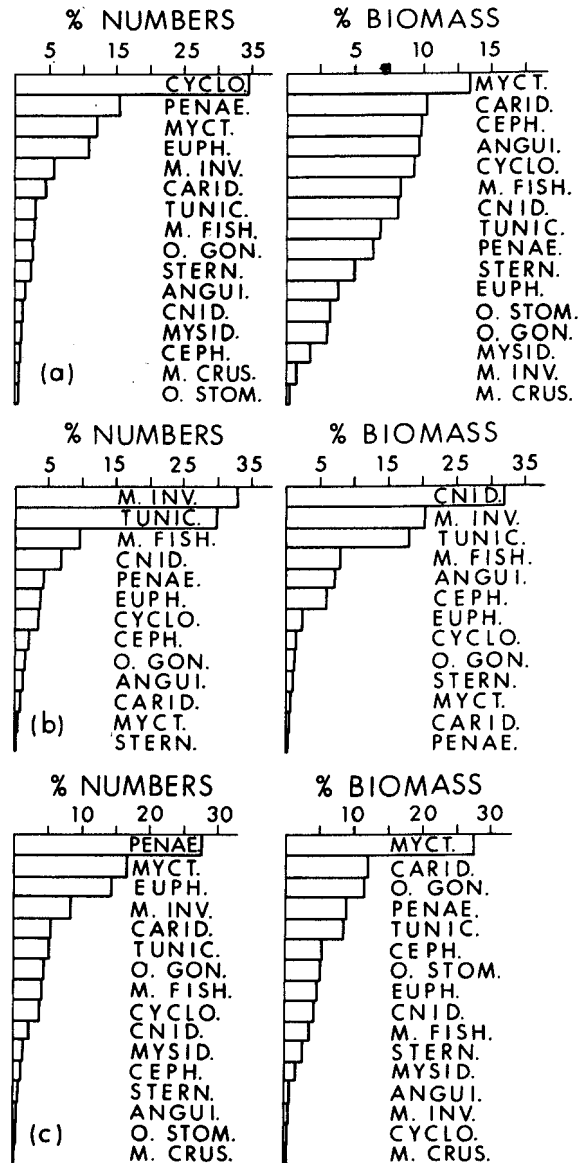


FIGURE 3.—Mean faunal composition by group as percent of total micronekton standing stock, number of organisms and wet-weight biomass. a. Deep-tows, 0-1,200 m. b. Shallow-day tows, 0-400 m. c. Shallow-night tows, 0-400 m. ANGUI. = Anguilliformes, CARID. = Caridea, CEPH. = Cephalopoda, CNID. = Cnidaria, CYCLO. = *Cyclothone*, EUPH. = Euphausiacea, M. CRUS. = Miscellaneous Crustacea, M. FISH. = Miscellaneous fishes, M. INV. = Miscellaneous invertebrates, MYCT. = Myctophidae, MYSID. = Mysidacea, O. GON. = Other Gonostomatidae, O. STOM. = Other Stomiatoidei, PENAE. = Penaeidea, STERN. = Sternoptychidae, TUNIC. = Tunicata.

The small euphausiids (<1 cm) which were sorted into the zooplankton group constituted 3.9 g wet weight and 831 individuals/100 m² ocean surface

for one deep tow (no. 183). This is about nine times the mean abundance of micronektonic euphausiids, but only one-fifth of the mean euphausiid biomass.

To establish a rough index of the contribution of neritic and meroplanktonic animals to the pelagic catch for future comparison, the standing stock of stomatopod larvae (otherwise included in the zooplankton group (Table 5)) was compared to the total micronekton stock (Table 6). The stomatopod concentration is large relative to shallow-day micronekton catches but quite small with respect to shallow-night and especially to deep-tow catches.

TABLE 6.—Mean standing stock of stomatopod larvae expressed as percent of total micronekton standing stock per 100 m² of ocean surface, number of organisms and wet-weight biomass.

Item	Day		
	0-1,200 m	0-400 m	Night 0-400 m
Number (%)	4.3	58.3	11.4
Biomass (%)	0.6	12.9	2.9

Diel Vertical Migration

Because there were no significant differences between standing stock estimates of deep-day and deep-night tows, we concluded that any trawl avoidance was not due to diel factors and that increased shallow-night catches were primarily

the result of vertical migration. Thus, the amount of vertically migrating micronekton was the difference between the shallow-day stock and the shallow-night stock (Tables 4, 5, 7). The percent migrating was then computed by dividing the amount migrating by the amount of micronekton deeper than 400 m during the day (deep-tow standing stock minus shallow-day stock). Percentages larger than 100 are considered sampling artifacts.

Of the total micronekton which resided deeper than 400 m during the day, 43% of the individuals with 47% of the biomass migrated into the upper 400 m at night (Table 7). This dramatic diel change in the catch rates of shallow tows is illustrated in Figures 4 and 5. The most numerous migrators were crustaceans, but most of the biomass was fishes. Between day and night tows the difference in composition of the 0- to 400-m layer of fauna is quite pronounced (Figure 3b, c).

The average weight per organism in each group for the 0- to 1,200-m deep water column was computed by dividing the mean group biomass in Table 5 by the mean number of organisms in the group shown in Table 4. The results are presented in Table 8 along with computations of the average biomass of individual migrators and non-migrators, based on the data in Table 7 and assuming that the non-migrator standing stock was the

TABLE 7.—Mean standing stock of vertically migrating micronekton, grams wet-weight biomass and number of organisms per 100 m² of ocean surface between 0 and 1,200 m, groups ranked by biomass and abundance. Percent migrating represents the portion of the group residing deeper than 400 m during the day which migrated into the 0- to 400-m layer at night.

Group	Biomass		Group	Abundance	
	g / 100 m ²	% migr.		No. / 100 m ²	% migr.
Myctophidae	69.66	106	Penaeidea	126.07	96
Caridea	30.12	60	Myctophidae	79.70	74
Other Gonostomatidae	28.83	199	Euphausiacea	62.22	68
Penaeidea	22.58	72	Caridea	25.82	67
Tunicata	15.78	56	Other Gonostomatidae	18.88	84
Other Stomiatoidei	13.36	86	Cyclothone	13.41	4
Cephalopoda	11.82	25	Mysidacea	8.73	88
Euphausiacea	11.42	65	Misc. fishes	4.77	43
Sternoptychidae	7.06	29	Sternoptychidae	3.94	17
Misc. fishes	6.81	18	Other Stomiatoidei	2.68	68
Mysidacea	4.42	50	Cephalopoda	2.35	49
Misc. Crustacea	1.09	100	Misc. Crustacea	1.88	46
Cnidaria	0.84	3	Anguilliformes	0.32	4
Cyclothone	0.74	2	Cnidaria	(!)	
Misc. invertebrates	(!)		Misc. invertebrates	(!)	
Anguilliformes	(!)		Tunicata	(!)	
Total fishes	125.59	50	Total Crustacea	224.72	82
Total Crustacea	69.63	64	Total fishes	123.70	26
Cephalopoda	11.82	25	Cephalopoda	2.35	49
Other invertebrates	11.40	21	Other invertebrates	(!)	
Total micronekton	218.43	47	Total micronekton	311.67	43

¹0-400-m day stock > 0-400-m night stock.

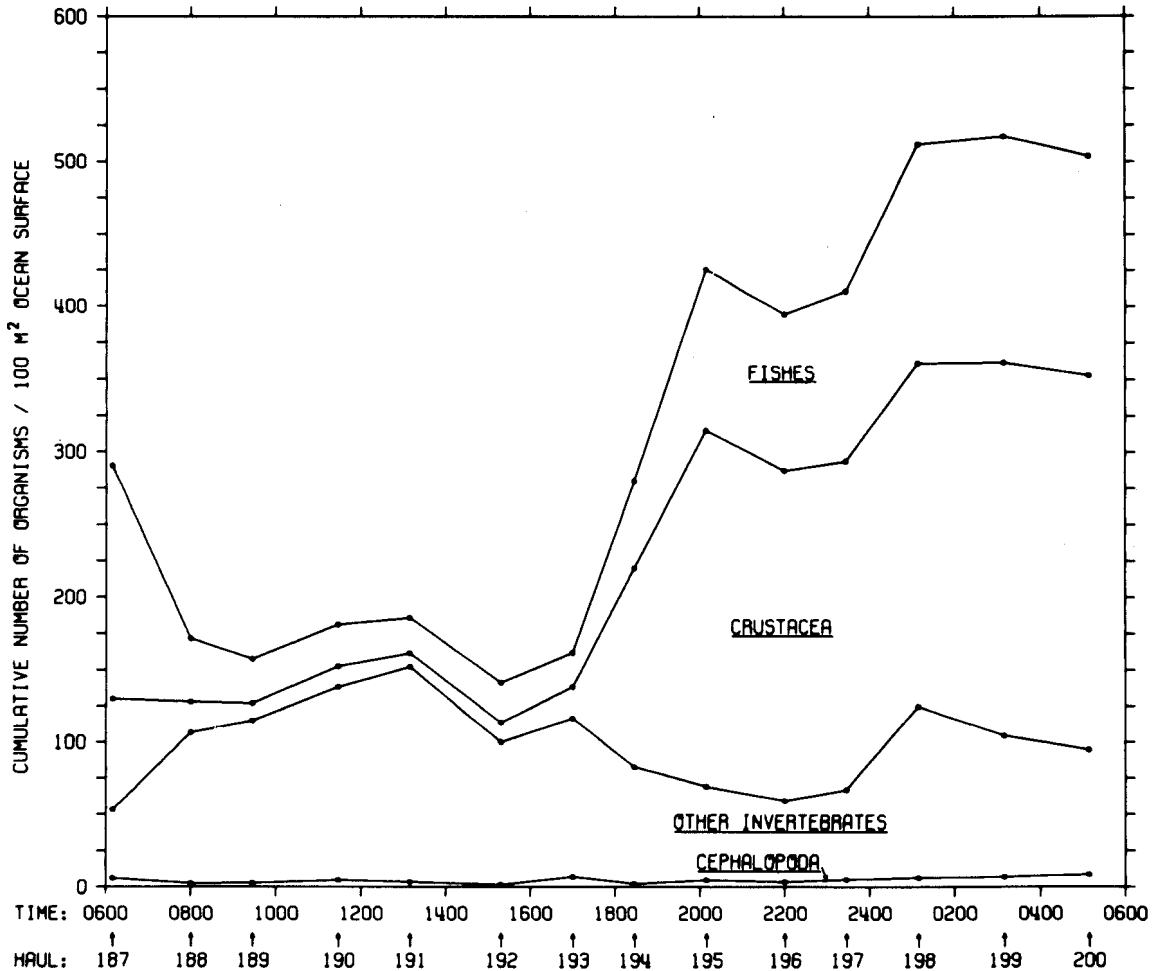


FIGURE 4.—Shallow-tow (0-400 m) standing stock of micronekton abundance over 24 h. Time is plotted for midpoint of each tow.

difference between the deep-tow stock and the migrator stock. In general, the average weight per migrating fish is greater than the weight of the non-migrators, while the opposite holds for the crustaceans and cephalopods, that is, the smaller-sized members of the groups migrate.

The occurrence of organisms larger than 10 g (wet weight) per individual was highly variable both with respect to abundance and biomass (Table 9). None occurred in the groups of *Cyclothone*, *Sternoptychidae*, *Penaeidea*, *Euphausiacea*, miscellaneous Crustacea, or miscellaneous invertebrates. The only large organism in shallow-day tows was one tunicate. In deep tows, large animals were less than 1% of the number of total micronekton but 30% of the biomass. With respect to biomass, about one-quarter of the total fishes,

one-eighth of the total crustacea, four-fifths of the Cephalopoda and one-half of the other invertebrates were made up of individuals larger than 10 g each. In shallow-night tows these proportions are smaller for all groups except other invertebrates which is about the same.

DISCUSSION

Restrictions

The interpretation of our data must be considered with several restrictions. Larger, highly mobile micronekton, especially fishes and cephalopods, probably avoid or escape the trawl (Pearcy and Laurs 1966; M. R. Clarke 1969; T. A. Clarke 1973, 1974) resulting in underestimation of

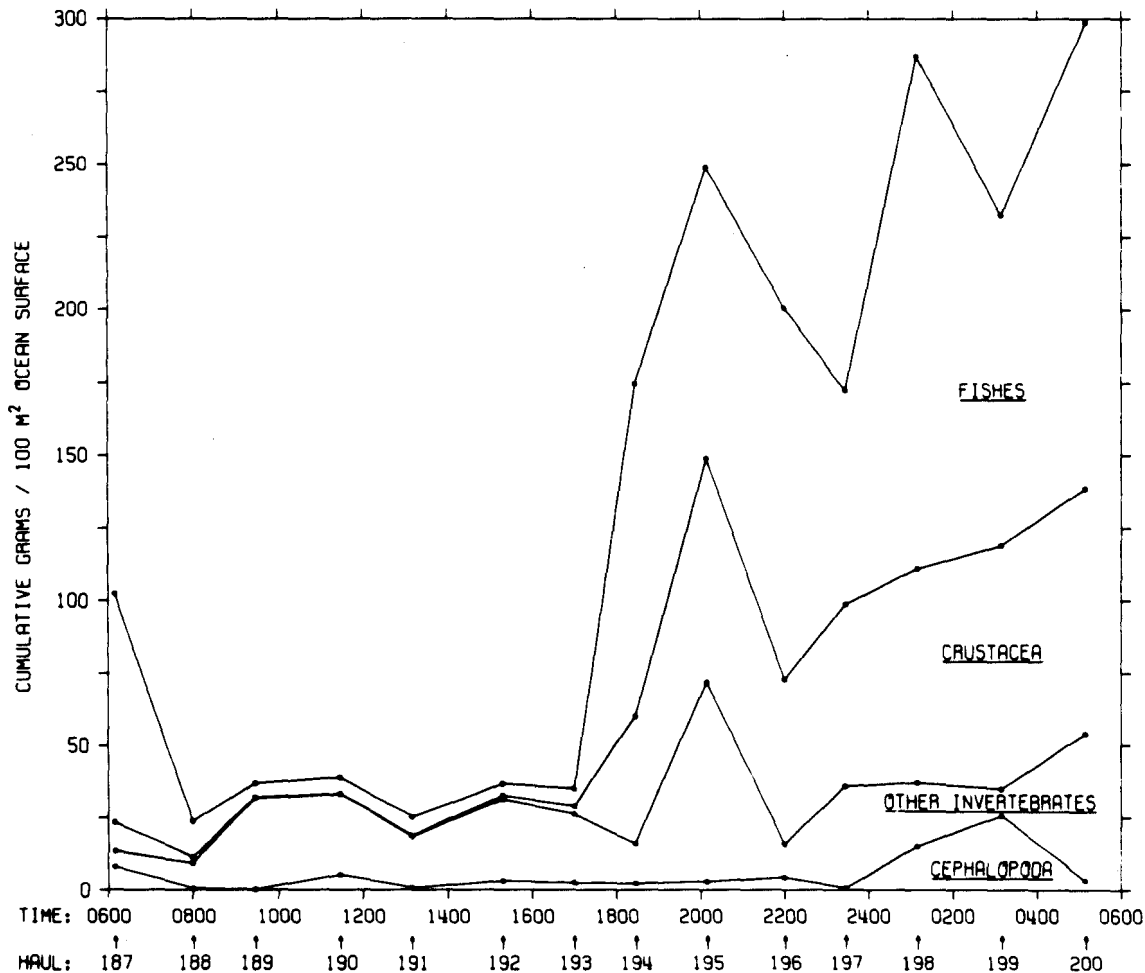


FIGURE 5.—Shallow-tow (0-400 m) standing stock of micronekton biomass (wet weight) over 24 h. Time is plotted for midpoint of each tow.

the numbers and especially biomass. In addition, pooling species into the 16 groups of Table 3 sometimes lumps vertical migrators with non-migrators, and primary carnivores with higher predators, blurring a precise ecological definition for a group. We feel, however, that our groups are adequate for a first overview of the micronekton fauna off Hawaii.

Our data may not represent standing stocks characteristic of the open ocean, and the possibility of an island effect should be considered. Oahu affects surface circulation up to 1,500 km downstream (Barkley 1971), but effects on plankton and micronekton standing stocks are not clear. An island mass effect has been observed off Oahu for phytoplankton (Gilmartin and Revelante 1974). King and Hida (1954, 1957a, b) found little

correlation between distance from Oahu and zooplankton standing stock, whereas other workers have found a decreasing standing stock with increasing distance from the island (Sette 1955; McGary 1955; Doty and Oguri 1956). Nakamura (1967) could detect no differences in mean zooplankton standing stock between windward and leeward Oahu samples, but windward samples consistently contained more decapods. We are not certain what island effects, if any, influence the leeward Oahu micronekton other than the occasional occurrence of some larvae of reef and benthic animals (e.g., stomatopods, crabs, fishes) which fall into the size range of micronekton as defined here.

Temporal fluctuations in micronekton standing stock pose an important caveat in evaluating our

TABLE 8.—Mean biomass per animal, grams wet weight, for the 0- to 1,200-m water column, vertical migrators (Table 7), and non-migrators (animals residing deeper than 400 m at night).

Group	0- 1,200 m	Migra- tors	Non- migra- tors
Myctophidae	0.61	0.87	(1)
Cyclothone	0.15	0.06	0.16
Other Gonostomatidae	0.58	1.53	(1)
Sternoptychidae	1.09	1.79	0.95
Other Stomiatoidei	3.97	4.99	1.77
Anguilliformes	4.22	(2)	(2)
Misc. fishes	1.50	1.43	2.12
Caridea	1.26	1.17	1.42
Penaeidea	0.23	0.18	0.76
Euphausiacea	0.19	0.18	0.20
Mysidacea	0.89	0.51	3.77
Misc. Crustacea	0.27	0.58	(1)
Cephalopoda	5.77	5.03	6.06
Tunicata	1.21	(2)	(2)
Cnidaria	(3)	(3)	(3)
Misc. invertebrates	0.06	(2)	(2)
Total micronekton	0.55	0.70	0.47
Total fishes	0.51	1.01	0.34
Total Crustacea	0.38	0.31	0.63
Other invertebrates	(2, 3)	(2, 3)	(2, 3)

¹0- to 400-m night stock minus 0- to 400-m day stock \geq 0- to 1,200-m stock.

²0- to 400-m day stock $>$ 0- to 400-m night stock.

³Siphonophores were not enumerated.

single-cruise data. In other parts of the world, investigators have reported seasonal biomass fluctuations of two- to sevenfold for some micronekton groups (Legand 1969; Blackburn et al. 1970; Tranter 1973), and abundance fluctuations of some species up to fifteen- to fortyfold (Percy 1964; Legand et al. 1970). Previous work in Hawaiian waters has demonstrated temporal variability in primary productivity (Gordon 1971:1132), epipelagic zooplankton standing stock (Nakamura 1967; Shomura and Nakamura 1969),

and such mesopelagic micronekton as myctophids (T. A. Clarke 1973) and stomiatoidei (T. A. Clarke 1974). The limited data available suggest at least twofold temporal fluctuations in micronekton standing stocks might be expected in Hawaiian waters. At this time we cannot predict seasonal oscillations in standing stock. Thus, until better seasonal data are available, our reported standing stock and faunal composition values should only tentatively be considered characteristic for Hawaii.

Standing Stock

On the basis of fish distributions, Amesbury (1975) has defined the 400- to 1,200-m depth range off Hawaii as the mesopelagic zone. Very few animals have been taken deeper than 1,200 m in opening-closing tows. Thus, standing stock values determined from our deep tows are probably reliable estimates for the micronekton of the whole water column except near-bottom waters.

In spite of the shortcomings, the data add considerably to our knowledge of micronekton especially because we sampled nearly the whole depth range of the fauna, used a fully lined net with small mesh, towed at a relatively high speed, sampled when the moon had a minimal effect on avoidance (cf. T. A. Clarke 1973), took several sample replicates, monitored sampling volume and depth, and determined standing stocks for all components of the catch. The general lack of diel-related avoidance agrees with the findings of T. A. Clarke (1973) and Atsatt and Seapy (1974) but is in contrast to the results of Percy and Laurs (1966).

TABLE 9.—Mean standing stock of micronekton larger than 10 g (wet weight)/individual, by group. a. No. organisms/100 m² ocean surface. b. Grams biomass/100 m² ocean surface. Standard deviation in parentheses.

a. Number. Group	Day			Night	b. Biomass, grams/100 m ² . Group	Day			Night
	0-1,200 m	0-400 m	0-400 m	0-400 m		0-1,200 m	0-400 m	0-400 m	
Myctophidae	0.08 (0.22)	0.00	0.10 (0.26)	0.38 (0.55)	Myctophidae	1.08 (3.25)	0.00	1.06 (2.82)	13.24 (20.52)
Other Gonostomatidae	0.15 (0.28)	0.00	0.18 (0.32)	0.00	Other Gonostomatidae	2.99 (6.41)	0.00	7.77 (16.46)	0.00
Other Stomiatoidei	0.31 (0.36)	0.00	0.00	0.00	Other Stomiatoidei	9.38 (11.25)	0.00	0.00	0.00
Anguilliformes	0.81 (0.83)	0.00	0.00	0.00	Anguilliformes	26.60 (36.06)	0.00	0.00	0.00
Misc. fishes	0.56 (0.88)	0.00	0.09 (0.25)	0.00	Misc. fishes	19.25 (37.84)	0.00	1.14 (3.01)	0.00
Caridea	0.53 (0.56)	0.00	0.00	0.00	Caridea	10.93 (12.41)	0.00	0.00	0.00
Mysidacea	0.22 (0.49)	0.00	0.27 (0.51)	0.54 (0.45)	Mysidacea	3.06 (6.71)	0.00	8.15 (15.80)	15.29 (14.92)
Cephalopoda	0.54 (0.47)	0.00	0.18 (0.49)	0.00	Cephalopoda	40.03 (49.24)	0.00	2.69 (7.11)	0.00
Tunicata	0.83 (1.57)	0.10 (0.23)	0.00	0.00	Tunicata	26.28 (12.95)	1.39 (11.54)	0.00	0.00
Cnidaria	0.52 (1.16)	0.00	0.00	0.00	Cnidaria	14.58 (35.30)	0.00	0.00	0.00
Total micronekton	4.62 (2.27)	0.10 (0.23)	1.76 (0.65)	0.67 (0.41)	Total micronekton	153.98 (54.80)	1.39 (11.54)	49.34 (14.81)	22.08 (20.18)
Total fishes	1.97 (1.21)	0.00	0.09 (0.25)	0.27 (0.51)	Total fishes	59.31 (58.50)	0.00	1.14 (3.01)	8.15 (15.80)
Total Crustacea	0.76 (2.76)	0.00	0.27 (0.51)	0.73 (0.77)	Total Crustacea	13.77 (17.36)	0.00	0.00	0.00
Cephalopoda	0.54 (0.47)	0.00	0.00	0.00	Cephalopoda	40.03 (49.24)	0.00	0.00	0.00
Other invertebrates	1.35 (1.74)	0.10 (0.23)	0.00	0.00	Other invertebrates	40.86 (44.70)	1.39 (11.54)	17.98 (18.57)	0.00
No. organisms	61	1	19	7					
No. tows	9	6	7						

We searched the literature for data to compare the standing stock and composition of micronekton off Hawaii with that of other regions. Few studies provided data from more than one sampling period; each used different gear and techniques, and all are subject to most of the restrictions cited previously. We feel that meaningful regional comparisons are premature until data on the temporal variability of the fauna are available from samples covering the entire depth range of the fauna.

Diel Vertical Migration

About one-half of the total micronekton wet-weight biomass in our study area appeared to migrate from day-depths greater than 400 m to night-depths shallower than 400 m. During the day, about 90% of the mean total micronekton standing stock biomass lived deeper than 400 m (Tables 5, 7). Because most vertically migrating fishes have a lower water content than non-migrators (Childress and Nygaard 1973) the percent of total micronekton dry weight which migrates would be even higher. The same probably holds for cephalopods. If migrators have shorter life spans and higher metabolic rates than non-migrators (cf. Childress and Nygaard 1973; T. A. Clarke 1973; Meek and Childress 1973), then the percent of the annual micronekton production represented by migrating animals would be especially high.

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LITERATURE CITED

- AMESBURY, S. S.
1975. The vertical structure of the micronektonic fish community off leeward Oahu. Ph.D. Thesis, Univ. Hawaii.
- ATSATT, L. H., AND R. R. SEAPY.
1974. An analysis of sampling variability in replicated mid-water trawls off southern California. *J. Exp. Mar. Biol. Ecol.* 14:261-273.
- BANSE, K., AND D. SEMON.
1963. On the effective cross-section of the Isaacs-Kidd mid-water trawl. *Univ. Wash. Dep. Oceanogr., Tech. Rep.* 88, 9 p.
- BARKLEY, R. A.
1971. Island wakes and their effects. *Pac. Sci. Congr. Proc.* 12(1):145.
- BLACKBURN, M., R. M. LAURS, R. W. OWEN, AND B. ZEITSCHSEL.
1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. *Mar. Biol. (Berl.)* 7:14-31.
- BROOKS, A. L., C. L. BROWN, JR., AND P. H. SCULLY-POWER.
1974. Net filtering efficiency of a 3-meter Isaacs-Kidd mid-water trawl. *Fish Bull., U.S.* 72:618-621.
- CHILDRESS, J. J., AND M. H. NYGAARD.
1973. The chemical composition of midwater fishes as a function of depth of occurrence off southern California. *Deep-Sea Res.* 20:1093-1109.
- CLARKE, G. L.
1971. Light conditions in the sea in relation to the diurnal vertical migrations of animals. *In* G. B. Farquhar (editor), *Proceedings of an international symposium on biological sound scattering in the ocean*, p. 41-50. *Maury Cent. Ocean Sci., Wash., D.C.*
- CLARKE, M. R.
1969. Cephalopoda collected on the SOND cruise. *J. Mar. Biol. Assoc. U.K.* 49:961-976.
- CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fish. Bull., U.S.* 71:401-434.
1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. *Fish. Bull., U.S.* 72:337-351.
- DEVEREAUX, R. F., AND R. C. WINSETT.
1953. Isaacs-Kidd midwater trawl, final report. *Scripps Inst. Oceanogr., Oceanogr. Equip. Rep.* 1, 18 p.
- DOTY, M. S., AND M. OGURI.
1956. The island mass effect. *J. Cons.* 22:33-37.
- FRIEDL, W. A.
1971. The relative sampling performance of 6- and 10-foot Isaacs-Kidd midwater trawls. *Fish. Bull., U.S.* 69:427-432.
- GILMARTIN, M., AND N. REVELANTE.
1974. The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. *J. Exp. Mar. Biol. Ecol.* 16:181-204.
- GORDON, D. C., JR.
1970. Chemical and biological observations at Station Gollum, an oceanic station near Hawaii, January 1969 to June 1970. *Hawaii Inst. Geophys., Tech. Rep.* HIG-70-22, 44 p.
1971. Distribution of particulate organic carbon and nitrogen at an oceanic station in the central Pacific. *Deep-Sea Res.* 18:1127-1134.

- GUNDERSEN, K., C. W. MOUNTAIN, D. TAYLOR, R. OHYE, AND J. SHEN.
1972. Some chemical and microbiological observations in the Pacific Ocean off the Hawaiian Islands. *Limnol. Oceanogr.* 17:524-531.
- HOPKINS, T. L.
1966. A volumetric analysis of the catch of the Isaacs-Kidd midwater trawl and two types of plankton nets in the Antarctic. *Aust. J. Mar. Freshwater Res.* 17:147-154.
- KING, J. E., AND T. S. HIDA.
1954. Variations in zooplankton abundance in Hawaiian waters, 1950-52. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 118, 66 p.
1957a. Zooplankton abundance in Hawaiian waters, 1953-1954. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 221, 23 p.
1957b. Zooplankton abundance in the central Pacific. Part II. U.S. Fish Wildl. Serv., Fish Bull. 57:365-395.
- LEGAND, M.
1969. Seasonal variations in the Indian Ocean along 110°E. VI. Macroplankton and micronekton biomass. *Aust. J. Mar. Freshwater Res.* 20:85-103.
- LEGAND, M., P. BOURRET, R. GRANDPERRIN, AND J. RIVATON.
1970. A preliminary study of some micronektonic fishes in the equatorial and tropical western Pacific. *In* W. S. Wooster (editor), Scientific exploration of the south Pacific, p. 226-235. Natl. Acad. Sci., Wash., D.C.
- MCGARY, J. W.
1955. Mid-Pacific oceanography, Part IV. Hawaiian offshore waters, December 1949-November 1951. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 152, 138 p.
- MEEK, R. P., AND J. J. CHILDRESS.
1973. Respiration and the effect of pressure in the mesopelagic fish *Anoplogaster cornuta* (Beryciformes). *Deep-Sea Res.* 20:1111-1118.
- NAKAMURA, E. L.
1967. Abundance and distribution of zooplankton in Hawaiian waters, 1955-56. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 544, 37 p.
- PEARCY, W. G.
1964. Some distributional features of mesopelagic fishes off Oregon. *J. Mar. Res.* 22:83-102.
- PEARCY, W. G., AND R. M. LAURS.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. *Deep-Sea Res.* 13:153-165.
- PUGH, P. R.
1974. The vertical distribution of the siphonophores collected during the SONDA cruise, 1965. *J. Mar. Biol. Assoc. U.K.* 54:25-90.
- SCHUERT, E. A.
1970. Turbulent diffusion in the intermediate waters of the north Pacific Ocean. *J. Geophys. Res.* 75:673-682.
- SETTE, O. E.
1955. Considerations of midocean fish production as related to oceanic circulatory systems. *J. Mar. Res.* 14:398-414.
- SHOMURA, R. S., AND E. L. NAKAMURA.
1969. Variations in marine zooplankton from a single locality in Hawaiian waters. U.S. Fish Wildl. Serv., Fish. Bull. 68:87-100.
- TRANTER, D. J.
1973. Seasonal studies of a pelagic ecosystem (meridian 110° E). *In* B. Zeitzschel (editor), The biology of the Indian Ocean, p. 487-520. Springer-Verlag, N.Y.