NET FEEDING IN MESOPELAGIC FISHES

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ABSTRACT

In an investigation of net feeding, 11 species of fish (5 gonostomatids, 6 myctophids) captured in a double-net Tucker trawl were examined. Stomach contents of fish retained by a coarse mesh "fish-catcher" in one net were compared to contents of fish which had accumulated with plankton in the cod end of the adjacent net. Out of 19 species-collection pairs (700 fish), there were significant ($P < 0.05$) differences in number of prey items in stomachs of only three species in five collections. Two pairs, fish from the cod end and in three pairs, those from the "fish-catcher," contained significantly more prey than fish from the adjacent trawl. There were little or no significant differences between trawls in number of fish scales, prey diversity, or prey size. These results suggest that literature data on diet of mesopelagic fishes is not heavily biased from net feeding and that existing collections can be used for feeding investigations.

Diet studies of mesopelagic fishes taken from plankton net cod ends of mid-water trawls could be seriously biased if fish feed extensively in the cod end. Indirect evidence for net feeding in pelagic shrimp has been presented by Judkins and Fleminger (1972) and in myctophid fish by Anderson (1967). DeWitt and Hopkins (in press) also suggest the possibility of net feeding in *Pleuragramma antarcticum*, a mid-water notothenioid fish. The problem of net feeding, though recognized by the above authors and others (e.g., Holton 1969; Collard 1970; Hopkins and Baird 1973), is largely unresolved; consequently the validity of published data on the diet of mesopelagic fishes is questionable. The present study was initiated to estimate the nature and degree of net feeding in the cod end of plankton net trawls by mid-water fishes to better judge the reliability of published information on diets of these fishes, and to determine if existing collections and present methods of collecting are adequate for trophic studies.

METHODS

Most of the material examined was collected from the eastern Gulf of Mexico with a double (side-by-side) closing Tucker trawl (Figure 1). One side of the trawl had an unmodified plankton net at the cod end. The mouth of the cod end plankton net of the adjacent trawl was fitted with a coarse mesh (1.1 cm stretched) conical "fish-catcher." In principal, the conventional trawl allowed the passage of fish into the cod end where plankton was concentrated; in the adjacent trawl fish were prevented from accumulating with plankton in the cod end by the fish-catcher. The body of the trawl was constructed of 1.1-cm stretched, knotless mesh. The cod ends for most collections were 333-μm mesh, 0.5-m diameter plankton nets. In collections subsequent to tow 152 (see Table 1), 1,050-μm mesh nets were substituted for the finer 333-μm mesh cod ends to improve the internal flow characteristics of the trawl. Other details of trawl design are in Hopkins et al. (1973). We have also included data from tow 98, a Caribbean sample, made with a single-net closing Tucker trawl (Hopkins et al. 1973). Fish gilled in the body of the trawl in this tow were compared with specimens from the cod end. Trawl hauls represented discrete depth samples which ranged from horizontal tows (± 10 m) to stepped oblique tows which sampled over a specified segment of the water column.

Fish were preserved in 10% Formalin[2] and subsequently transferred to 40% isopropyl alcohol. Specimens selected for analysis (370 from cod end; 332 from fish-catcher) were measured to the nearest millimeter (standard length, SL) prior to stomach removal. Contents of the pigmented distensible region posterior to the esophagus and anterior to the intestine were identified to genus when possible, measured, and counted (see Hopkins and Baird 1973; Baird et al. 1975). Prey

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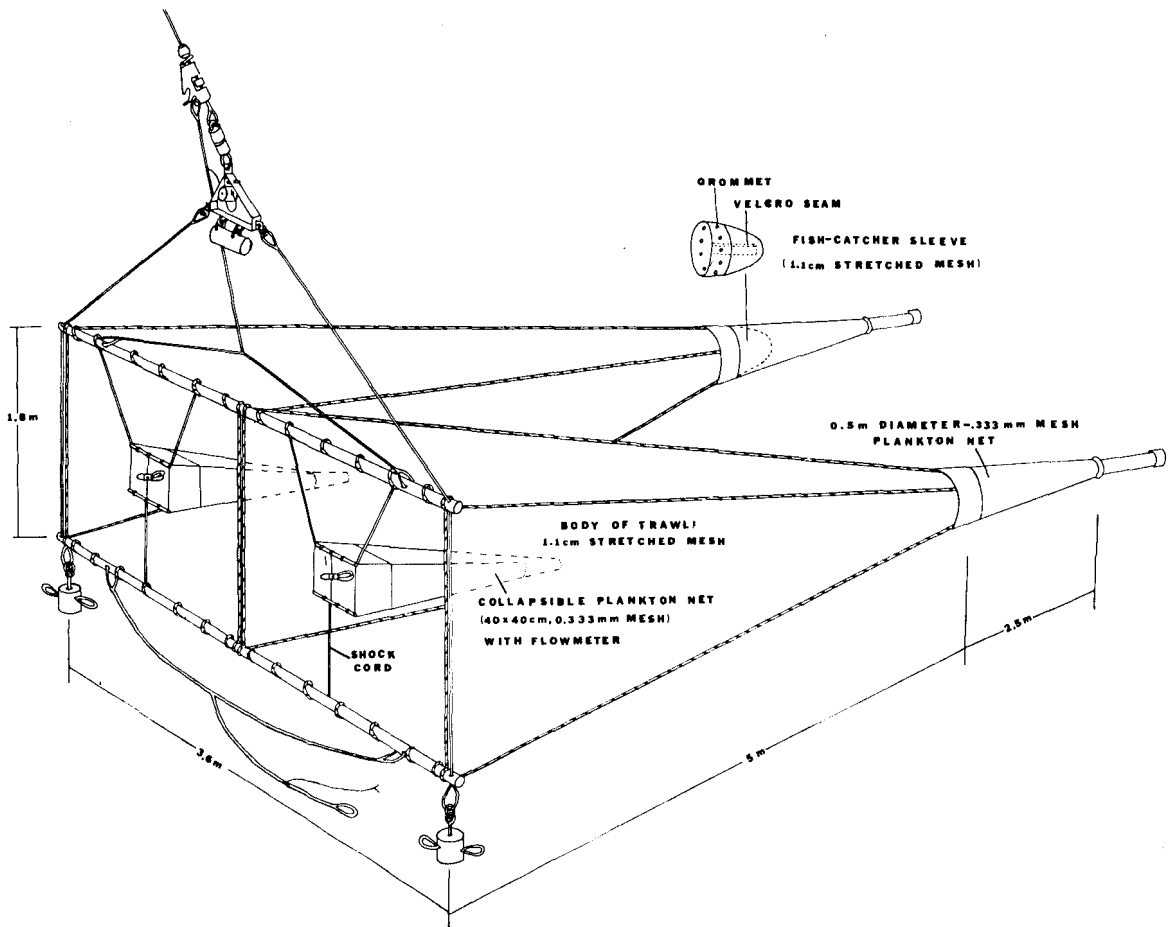
FIGURE 1.—Double-net closing Tucker trawl showing modified (fish-catcher sleeve) and conventional cod ends.

items contained in the mouth, pharyngeal region, esophagus, or intestine were not included in the analysis. Student's *t*-test was used for most statistical comparisons, the distributions being first tested for skewness and kurtosis (Sokal and Rohlf 1969). If the data to be tested were not normally distributed, then a log or square root transform was applied and the resulting distributions re-tested for skewness and kurtosis. *F*-tests were used to determine homogeneity of variances; the few exceptions to homogeneity will be discussed under the appropriate section. Standard chi-square tests were used to test the similarity of prey size distributions.

To compare prey availability in the trawl cod end with fish stomach contents, plankton was examined from tows 135, 137, and 141-144 (Table 2). Trawl mouth plankton net collections were used in preference to cod end catches because of possi-

ble losses of small plankton incurred in sorting larger fish and shrimp from the latter. Both cod end and trawl mouth nets for these particular tows had the same mouth area (0.2 m^2) and mesh size (333 μm) and were considered comparable in fishing characteristics, at least for the smaller plankton typically found in fish stomachs. Trawl mouth plankton collections for tow 137 were not available, consequently the catch from the cod end net of the fish-catcher side of the trawl was substituted. This particular cod end collection had not been "rough sorted" for larger organisms and was in excellent condition.

Zooplankton was identified, usually to genus, and counted in each of two subsamples. One plankton net collection (two subsamples) was analyzed for tows 135, 137, and 142 while two collections (four subsamples) were examined for the remaining tows. The mean number of

TABLE 1.—Comparison of diet characteristics of fish examined in net feeding investigation. F = "fish-catcher" side of double trawl; P = unmodified side of double trawl (see Figure 1); G = gilled in meshes of body of trawl; t-tests:* = $P<0.05$, ** = $P<0.025$, *** = $P<0.01$, **** = $P<0.005$.

Species	Trawl no.	Depth (m)	Time of collection	Trawl side	No. fish	Fish size (mm) x̄ (range)	Prey items per stomach x̄ (range)	Prey size (mm) x̄	Prey diversity (taxa)	No. fish scales[2]
			Night (post-midnight)[1]							
Argyropelecus aculeatus	144	156-197	0220-0515	F	6	29 (24-36)	2.8 (0-8)	2.7	5	0
				P	8	31 (22-38)	6.4 (1-14)	3.7	15	2
Benthosema suborbitale	137	94	0227-0543	F	27	28 (23-31)	3.0 (0-7)	1.9	17	0
				P	25	28 (25-33)	3.5 (0-15)	2.0	20	6
Ceratoscopelus warmingi	137	94	0227-0543	F	25	33 (28-52)	8.5 (2-18)	1.8	42	0
				P	25	32 (28-48)	10.1 (1-28)	1.8	52	2
Gonostoma elongatum	144	156-197	0220-0515	F	23	96 (71-113)	2.7 (0-7)	6.2		
				P	29	97 (68-117)	2.0*(0-5)	5.4		
Lampanyctus alatus	141	128	0240-0350	F	32	39 (29-46)	5.8 (0-13)	2.9	26	1
				P	32	39 (28-45)	7.3***(1-17)	3.2	39	7
Lepidophanes guentheri	137	94	0227-0543	F	36	50 (38-58)	6.6 (0-19)	4.0	31	9
				P	35	50 (37-58)	7.2 (0-17)	3.0	35	3
Notolychnus valdivae	141	128	0240-0350	F	10	20 (17-22)	2.7 (0-6)	2.9		
				P	39	20 (16-23)	2.6 (0-9)	2.5		
Valenciennellus tripunctulatus	152	397-450	0140-0545	F	8	28 (25-31)	2.3 (0-5)	2.7	6	0
				P	6	28 (25-32)	2.8 (2-4)	2.9	5	0
			Night (pre-midnight)							
Ceratosropelus warmingi	161	90-130	2047-2321	F	20	38 (32-45)	5.5 (0-13)	2.3		
				P	13	34*(29-45)	3.5****(0-7)	2.3		
Diaphus dumerlii	173	30-130	2108-2355	F	6	51 (37-66)	17.7 (7-29)	3.7	22	0
				P	6	48 (41-63)	11.3 (2-22)	4.1	17	0
Cyclothone pallida	147	781-844	2130-0100	F	23	44 (33-52)	0	0	0	0
				P	24	43 (28-52)	0.04 (0-1)	4.5	1	0
Lampanyctus alatus	167	60-130	2102-2350	F	30	41 (34-48)	3.2 (0-9)	3.9		
				P	24	38 (29-48)	4.8*(0-16)	4.2		
Lepidophanes guentheri	167	60-130	2102-2350	F	7	55 (48-59)	9.7 (3-19)	4.4	12	1
				P	7	33 (44-59)	11.7 (2-46)	5.2	12	0
Valenciennellus tripunctulatus	143	257-348	2117-2352	F	6	24 (23-27)	10.2 (3-16)	1.8		
				P	24	24 (21-29)	10.3 (0-23)	1.7		
			Day (morning)							
Argyropelecus hemigymnus	142	363-545	0920-1240	F	18	23 (17-29)	4.2 (0-11)	1.8		
				P	11	26 (19-33)	5.2 (0-11)	1.7		
Gonostoma elongatum	145	660-1,000	0830-1130	F	12	108 (93-120)	3.0 (1-5)	6.6	8	0
				P	10	110 (99-130)	1.3*(0-4)	4.2	6	0
Lepidophanes guentheri	98	570-705	0755-1112	F	15	46 (38-54)	9.1 (0-22)	4.1		
				G	19	49 (39-62)	9.3 (1-27)	3.7		
Valenciennellus tripunctulatus	142	363-545	0920-1240	F	19	27 (21-30)	3.7 (0-11)	2.1	12	0
				P	22	27 (24-31)	3.8 (9-10)	2.2	12	0
			Day (afternoon)							
Valenciennellus tripunctulatus	135	340-627	1435-1830	F	9	25 (21-29)	10.9 (0-16)	2.4	14	0
				P	11	24 (18-28)	11.5 (2-24)	2.0	13	0

[1]Time of tow initiation.
[2]Fish scales only; no other fish remains present.

plankters counted in each subsample was 775 (range: 453-1,079).

RESULTS

Fish Size Distribution

Because of possible relationships between number of items in stomachs (also other diet characteristics) and size of predator (e.g., Nesis 1965; Hopkins and Baird 1973), the mean length and size range of fish from each trawl were compared for each pair (Table 1). There were no sig-

nificant differences in mean length (t-test, $P>0.05$) in 18 of 19 pairs. For the single exception, *Ceratoscopelus warmingi* from tow 161, the mean size of fish from the catcher size was larger ($P<0.05$; x̄ (SL): 38 vs. 34 mm). However, since the distributions had considerable overlap, this set was included in the study.

Prey Abundance in Stomachs

It was necessary to apply a square root transform ($\sqrt{X+0.5}$) to the data on number of prey per stomach since the high frequency of empty

TABLE 2.—Relative abundance of principal (top 3) food items in fish stomachs and in plankton taken concurrently with fish, with 333-μm mesh nets mounted in the mouth of the double trawl (see Figure 1): F = "fish-catcher" set of fish; P = cod end plankton net set.

Species	Tow	Top 3 prey items in stomachs	Numerical abundance of prey in stomachs (%)			Numerical abundance in plankton nets (%)	Top 3 items in plankton nets	Numerical abundance in plankton nets (%)
			F	P	$\bar{x}$			
Argyropelecus	142	Oncaea	45	42	43.5	12	Eucalanus	41
hemigymnus		Conchoecinae	17	23	20.0	5	Oncaea	12
		Eucalanus	12	9	10.5	41	Scolecithricidae	10
Benthosema	137	Oncaea	23	24	23.5	9	Conchoecinae	12
suborbitale		Pleuromamma	21	17	19.0	9	Pleuromamma	9
		Conchoecinae	11	10	10.5	12	Clausocalanus	9
Ceratoscopelus	137	Limacina	13	17	15.0	3	Conchoecinae	12
warmingi		Conchoecinae	12	14	13.0	12	Pleuromamma	9
		Siphonophores	12	11	11.5	2	Clausocalanus	9
Gonostoma	144	Stylocheiron	16	21	18.5	2	Sagitta	19
elongatum		Pleuromamma	13	33	23.0	1	Conchoecinae	18
		Conchoecinae	13	9	11.0	21	Oithona	14
Lampanyctus	141	Pleuromamma	23	25	24.0	4	Oithona	14
alatus		Stylocheiron	16	13	14.5	4	Sagitta	8
		Conchoecinae	8	6	7.0	8	Conchoecinae	8
Lepidophanes	137	Pleuromamma	25	31	28.0	9	Conchoecinae	12
guentheri		Euphausia	14	6	10.0	<1	Pleuromamma	9
		Conchoecinae	11	9	10.0	12	Clausocalanus	9
Valenciennellus	142	Oncaea	24	12	18.0	12	Eucalanus	41
tripunctulatus		Pleuromamma	19	22	20.5	3	Oncaea	12
		Euchaeta	10	(6)	8.0	1	Scolecithricidae	10
		Eucalanus	(3)	15	9.0	41		
Valenciennellus	143	Oncaea	40	38	39.0	9	Pleuromamma	15
tripunctulatus		Pleuromamma	23	25	24.0	15	Conchoecinae	14
		Conchoecinae	6	8	7.0	14	Oithona	10
Valenciennellus	135	Eucalanus	19	16	17.5	20	Pleuromamma	23
tripunctulatus		Pleuromamma	16	14	15.0	24	Eucalanus	20
		Euchaeta	10	(9)	9.5	<1	Euphausia	7
		Oncaea	(3)	19	11.0	1		

stomachs resulted in significant skewness in the distributions of many untransformed data sets. In three set comparisons there were significant differences (F-tests, 0.05 >P >0.025) in variance (Benthosema suborbitale, tow 137; C. warmingi, tow 137; Lampanyctus alatus, tow 167). In these cases, tests comparing means of normal distributions when population variances are unequal were applied as described by Johnson and Leone (1964:226).

There were significant (t-tests, P<0.05) differences in 5 of 19 comparisons of number of prey items per stomach. Lampanyctus alatus in two collections contained more prey items per individual in fish taken from the plankton net cod end (tow 141: 0.025 >P >0.01; tow 167: 0.05 >P >0.025). However, for Gonostoma elongatum in two sets (tows 144, 145: 0.05 >P >0.025), and C. warmingi in one set (tow 161:P<0.005), individuals from the fish-catcher side averaged more prey per stomach. Because of possible diurnal feeding periodicity in mid-water fishes (Anderson 1967; Holton 1969; DeWitt and Cailliet 1972; Baird et al. 1975), fish entering the trawl at different periods in their feeding cycle may be satiated or have a different predisposition to feed in varying

degrees. The five sets of fish showing significant differences in number of food items, however, are not conspicuously grouped in any single time period (see Table 1) and no general relationship is apparent in our results between time of capture and relative abundance of prey in fish from either side of the trawl.

Mean Prey Size

In 8 of 19 data sets, mean prey size was smaller in cod end fish. The major size modes were coincidental in all 19 set comparisons as judged from visual inspection. A t-test of the grand means (mean of 19 individual means for each cod end type), however, revealed no significant (P>0.05) difference in mean size of food item for fishes in either side of the trawl (variance of means homogeneous). Though the sensitivity of this test is weakened to some degree by comparing different species of fish collected at different times, a strong bias in prey size resulting from net feeding is not apparent.

Prey size distributions for 14 paired sets were also compared using the contingency chi-square test. Significant (P<0.05) differences were found

in only two pairs: *Lepidophanes guentheri*, tow 167 ($P<0.001$) and *Valenciennellus tripunctulatus*, tow 135 ($0.005>P>0.001$). In the former, those individuals from the cod end took more prey items in smaller size classes while in the latter the reverse occurred. We have no simple explanation for these results. It is difficult to attribute them, however, to net feeding since other diet characteristics tested showed no significant differences for these same sets. Additionally, paired samples of the same species from other collections revealed no significant differences.

Prey Diversity

In comparison to the coarse mesh fish-catcher, the unobstructed cod end net of the adjacent trawl contained a much greater variety of plankton and consequently a more diverse potential food source for net feeding. A comparison was made of diversity of food items in stomachs of fish from each side of the trawl using 12 (of 19) species-pair collections represented by sets of approximately equal numbers of individuals for each cod end type. Total diversity was scored for each set of fishes, yielding two diversity values for each species-pair collection. Diversity scores were then summed to give grand means for each cod end type.

On the basis of a *t*-test on $\log_{10}$ transformed data, no significant ($P>0.05$) difference was indicated for the two cod end types though total diversity was considerably greater in fishes from the plankton net cod end in some sets (e.g., *Argyropelecus aculeatus*, tow 144; *L. alatus*, tow 141).

Fish Scales

Anderson (1967), in his analysis of the diet of *Bathylagus stilbius*, frequently encountered fish scales in stomachs yet no other remains of fish of the size indicated by the scales. This, in addition to the absence of scales in intestines and the occurrence of scales and copepods in the mouths of fish, he considered as evidence of net feeding. In the present study, fish in half the sets of samples (6 of 12) for which data are presented contained no fish scales. In four of the remaining six pairs, more scales were found in fish from the cod end where scales would be expected to accumulate during the course of a tow, but none of the differences were significant (*t*-test on $\sqrt{X+0.5}$ transformed data; $P>0.05$).

The occurrence of fish scales in stomachs does not necessarily stem from predation on smaller fish or from eating scales abraded from fish within the trawl. Fish scales appear to be common in the water column and thus available as separate forage items. In a series of paired 30-liter bottle casts made between 0 and 1,000 m in August 1972, in the eastern Gulf of Mexico where most of the fish examined were taken, scales occurred in collections (60 liters/sample) from 7 of 15 depths sampled at densities of 17-83 per m^3. Scales ranged from 0.5 to 5 mm in diameter. No fish were taken in the sample bottles and the probability of contamination from other sources appears low.

Taxonomic Composition of Stomach Contents and Plankton

Table 2 presents the principal taxonomic components of prey found in nine sets of fish from both sides of the trawl. The principal diet item was the same in both sets of fish in six of nine collections, the same prey constituted the top three food items by number in seven of nine collections and the prey taxa were in the same rank order in five of nine collections. The principal three prey taxa in fish from either side of the trawl were within $\pm3\%$ of the mean value for both sides from each tow in 25 of 29 food item comparisons and all values were within $\pm10\%$ of the means. These results show that the taxonomic composition of at least the principal components of the diet was similar in fish from both sides of the trawl for all comparisons.

Comparison of food items in stomachs of fish from the cod end, where net feeding is assumed mostly likely to occur, with plankton catches reveals little similarity in the top three taxonomic components. In none of the nine collections was the principal taxon the same in either the plankton net catch or in the stomachs of fish from the cod end. Of particular importance are tows 137, 141, 144, 152, and 161 which sampled relatively narrow depth zones and consequently were potentially less influenced by vertical stratification of plankton. Also, three species of fish collected in the same haul (tow 137) each contained a different principal food item, none of which matched the most abundant taxon in the cod end plankton catch. The major diet components for *Benthosema suborbitale*, *C. warmingi*, and *L. guentheri* from tow 137 were *Oncaea*, *Limacina*, and *Pleuromamma*; the most abundant plankton in the cod end net were ostracods (Conchoecinae). This particular haul was

a horizontal tow in which a discrete depth was maintained throughout.

DISCUSSION

While studies of the behavior of mesopelagic fishes in small mid-water trawls used for research are nonexistent, there is considerable information available on fish behavior in larger commercial trawls of many kinds (e.g., Ben-Tuvia and Dickson 1968). Generally, fish move in front of or away from the walls of the trawl until they are exhausted and are collected in the cod end. Mesopelagic fishes from trawl cod ends often show signs of abrasion (Harrisson 1967); consequently, the likelihood of active and extensive net feeding would appear low. Several authors (e.g., Collard 1970; Hopkins and Baird 1973) have suggested that trauma induced by stress conditions in the trawl environment would operate against active feeding behavior. Reflexive gulping or "pseudo" feeding behavior, however, resulting in the ingestion of significant amounts of prey from the plankton rich cod end is a potential mechanism whereby stomach contents could be biased by net feeding. Several studies have revealed diel periodicity in feeding in mid-water fishes which indicates that at certain times, at least, net feeding cannot be extensive (Holton 1969; DeWitt and Cailliet 1972; Baird et al. 1975).

The possibility of fishes foraging in front of the cod end or fish-catcher can also be evaluated. At standard trawling speeds (3.7-4.6 km/h) the trawl moves at a rate of 1.0 to 1.3 m/s. For those epipelagic species which have been examined, foraging and cruising speeds range from about 1 to 4 body lengths per second and maximum burst speeds are on the order of 10 to 30 body lengths per second (e.g., Blaxter 1969; Baird et al. 1975). Assuming similar swimming capabilities for mid-water fishes and a fish size of 3 inches (76 mm), a conservative estimate of foraging speeds should be less than 0.3 m/s and burst rates of 0.8 to 2.3 m/s. All of the species examined here were less than 76 mm in length except *G. elongatum* which may have somewhat limited swimming capabilities (Marshall 1971). In view of the swimming speeds required, extensive foraging in front of the cod end appears remote. In addition, the data from *L. guentheri* (tow 98), where prey of individuals gilled in the net were compared with those from the cod end, failed to reveal indications of net feeding.

The present results support the contention that if net feeding does occur, it is not extensive in the relatively small fragile fishes typical of the oceanic mesopelagic enrivonment. Only the data on prey abundance in stomachs of *L. alatus* could be construed as statistical evidence of net feeding. In both of these collections, however, mean size of prey items and taxonomic composition of diet were very similar in both sets of fish, while the diet showed little agreement in terms of principal taxonomic components (Table 2) with plankton in the cod end, as might be expected from net feeding. In three collections (tows 144, 145, 167), *G. elongatum* (2 sets) and *C. warmingi* (1 set) from the "control" side contained more food items than fish from the cod end. Here again comparisons of mean prey size, taxonomic composition of diet, and major taxa in diet with that in cod end plankton samples failed to reveal evidence of net feeding. Furthermore, there were often substantial differences between principal taxonomic components of diet and plankton from cod end catches from the same haul. Mean prey size (with two exceptions) and composition of principal taxa of diets were nearly identical for all sets of comparison which further indicate the limited nature of net feeding in this study.

The use of fish scales as a criterion for net feeding poses a number of difficult problems. Our hydrocasts reveal, for instance, that fish scales occur naturally in the water column. Further, several studies of both marine and freshwater teleost fishes have shown that scales (probably also the covering mucous and epidermis) can serve as a major component of the diet, appear to be easily digested, and may possibly have considerable nutritive value (e.g., Roberts 1970, 1973; Carr and Adams 1972, 1973). Scales were relatively rare in stomachs examined here but did occur in fishes from both sides of the trawl. Since scales are present in the natural environment, may have nutritive value, and are possibly easily seen, captured, and eaten, they could serve as a natural food source or provide appropriate stimuli to elicit ingestion. Until more evidence is obtained concerning the role of scales in the natural diets of fishes and their abundance in oceanic environments, the presence of scales in the stomachs of mid-water fishes cannot be used with assurance as an indicator of net feeding.

Because of the difficulty of replicating trawl conditions and obtaining sufficient material for analysis, the variability in distributions of mid-

water fishes with respect to time and space, and possible variations in feeding cycles, the present collections are not ideal in all respects. The study did include representatives of most of the major groups of common mesopelagic fishes from a variety of depths and times, and the results may be expected to be broadly applicable to many mid-water environments. Considering the simul-taneous time-depth collections with the double trawl of both "control" fish and those with the opportunity to ingest food in the cod end, this study provides the first reasonably good test of net feeding in mesopelagic fishes. The relatively small differences in the mean number and taxonomic composition of prey items in most sets of stomachs are encouraging. The results presented here sug-gest that the published literature on the diets of mesopelagic fishes is not seriously biased by net feeding and that existing collections can be used for trophic investigations.

ACKNOWLEDGMENTS

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