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COMPARATIVE CAPTURES OF PELAGIC CEPHALOPODS BY MIDWATER TRAWLS

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SYNOPSIS

The captures of pelagic cephalopods by the 3 m Isaacs-Kidd midwater trawl (IKMT), the 8 m^2 rectangular midwater trawl (RMT 8), and the small (1400 mesh) Engel trawl (EMT) are compared. The sampling site was a one-degree square area in the North Atlantic Ocean east of Bermuda known as Ocean Acre. The IKMT and the RMT 8 were equipped with closing devices. Comparative samples were taken on the same cruise or at least during the same season of the year. The comparisons were made on net captures taken at 13 standardized depth increments from the surface to 1250 m for both day-time and night-time. Comparisons were developed for catch rate (standardized to number of specimens captured per hour of trawling), species composition, size distribution, and co-occurrence of species.

The comparison of IKMT and the RMT 8, nets with nearly equivalent mouth openings, indicates that the IKMT catches slightly larger specimens of the same species than the RMT 8. The RMT 8, however, catches more specimens per hour of a given species than the IKMT, and it tends to catch a greater diversity of species.

The Engel trawl, a net with a much larger area of mouth opening than the other nets, catches a significantly greater number of species, more specimens of each species, and very much larger specimens than either the IKMT or the RMT 8.

INTRODUCTION

The development of the Isaacs-Kidd midwater trawl (IKMT) in 1953 (Isaacs & Kidd, 1953) initiated a new era in sampling and analysis of midwater macroplanktonic and nektonic organisms. Since that time several modifications of the IKMT have appeared (e.g., Aron, Raxter, Noel & Andrews, 1964) and other midwater trawls, both high-speed and low-speed varieties, have been constructed (e.g., Schärfe, 1960; McNeely, 1963; Clarke, 1969a; Baker, Clarke & Harris, 1973). Summaries on the development and use of the broad spectrum of midwater sampling gear are presented in Harrison (1967) and in Gehringer & Aron (1968).

A number of studies comparing catch characteristics of various kinds of midwater trawls have been conducted with analyses concentrated primarily on fishes, crustaceans, and plankton (e.g., Aron, 1962; King & Iverson, 1962; Berry & Perkins, 1966; McGowan & Fraundorf, 1966; Badcock, 1970; Friedl, 1971).

No specific comparative study of cephalopods from different midwater trawls has been undertaken. Those reports in which comparisons have been attempted are concerned primarily with the vertical distribution of pelagic cephalopods. In an initial study, Clarke (1969b) reported catches of cephalopods taken during the SOND cruise in a 1 m ring net (N113H) and a 3 m IKMT, each equipped with a closing device in the form of a catch-dividing bucket (Foxton, 1963, 1969). Catches were recorded only as numbers of individuals captured in each net-tow; that is, they were not standardized for fishing effort (e.g., numbers per hour of trawling). The N113H is a plankton net, and therefore caught larvae primarily, while the 3 m IKMT, designed to sample macroplankton and nekton, caught juveniles primarily. Clarke (1969b: 976) concluded that a thorough sampling of the cephalopod fauna was "very inadequate" using either net. Because of inherent limitations of the catch-dividing bucket system on the 3 m IKMT, principally contamination (Foxton, 1969; Clarke, 1969a and pers. comm.), sampling with this device was terminated, and the rectangular midwater trawl (RMT) with a mouth-closing device was developed (Clarke, 1969a; Baker *et al.*, 1973).

Clarke & Lu (1974) described the vertical distribution of cephalopods at 30°N 23°W utilizing specimens captured with the RMT, the IKMT with catch-dividing bucket, open IKMT, and open British Columbia midwater trawl. The number of specimens captured for each species was recorded, but again captures were not standardized for fishing effort, although tows ranged from less than half an hour to over four hours in duration. The RMT tows were taken during a one-week period in March–April, 1972, while all remaining comparative tows were taken during August, September and October, 1961, and April and June of 1962. Although differences in catch between the similarly sized IKMT and RMT were thought to be due to net selection (Clarke & Lu, 1974: 983), the wide variability in years between samples, the different seasons, and the absence of standardization for fishing effort, make meaningful comparisons difficult.

The vertical distribution of pelagic cephalopods was reviewed by Roper & Young (1975) based primarily on midwater trawling programs using a non-closing 3 m IKMT, the Ocean Acre 3 m IKMT with closing device and a mouth-closing "Tucker trawl", similar to the RMT 8. Captures were analysed by catch rate, but no direct comparisons between trawls were attempted.

The studies upon which this paper is based were also designed to determine vertical distributions of nektonic forms. As several different types of gear were employed, however, an opportunity arose to determine fishing characteristics in a comparative manner with regard to cephalopod sampling. Since each design of mid-water trawl samples the fauna differently, the ecological information derived is biased by net type. The relative sophistication of the IKMT and RMT systems and methods gave the opportunity to make valid comparisons and so attempt initial evaluation of the sampling effectiveness of the nets involved. Thus, a comparison of the cephalopods captured in a 3 m IKMT, and RMT 8, and a small (1400 mesh) Engel trawl (EMT) is presented here.

GEAR AND METHODS

The results of this study are particularly important because the IKMT and RMT *in situ* monitoring systems permitted precise depth placement and control of the nets and this resulted in refined sampling strategies that could be strictly adhered to, consequently allowing a reasonable degree of comparability.

Despite this sophistication of the gear and methods, it is recognized that certain limitations may be imposed by the complex environment that prohibit complete realization of the ideal program. For example, sampling with different nets could not be simultaneous, environmental conditions may not be stable during a given season from year to year, filtration rates may not be consistent because of differences in ships, weather conditions or current configurations. Nevertheless, these programs provide the most comprehensive and comparative data available on midwater cephalopod populations to date and should form a stimulus for further analyses.

The 3 m Isaacs-Kidd midwater trawl

The sampling program of which these studies formed a part, took place in a one-degree square area east of Bermuda, centered at 32°N 64°W, known as the Ocean Acre. The Ocean Acre program (1967–1972) utilized a 3 m IKMT equipped with the discrete-depth plankton sampler, a closing device at the cod end of the net (Aron *et al.*, 1964). Details of the methods and equipment of the Ocean Acre program are presented in Gibbs & Roper (1970) and in Gibbs, Roper, Brown & Goodyear (1971).

Briefly, the IKMT cod-end closing device consists of a 15 cm diameter, four chambered cylinder (Aron *et al.*, 1964). This trawling system allows the collection of three sequential samples from one depth; the fourth chamber contains the sample captured during oblique retrieval of the net from the fishing depth to the surface. The gates separating the chambers are closed by a solenoid-actuated triggering mechanism upon receipt of a frequency-coded signal via the conductor towing cable. During the later stages of the 14-cruise Ocean Acre program a system of simultaneous, *in situ* monitoring of depth of net, ambient temperature, light intensity, and flow of water through the net was employed.

The mesh size (bar measure) of the 3 m IKMT liner was 6·0 mm throughout with a 3 m-long 0·75 mm cod-end net. The area of the opening of the mouth during the fishing procedure was 7·44 m^2. Brooks, Brown & Scully-Power (1974) determined experimentally that the 3 m IKMT, apparently not equipped with a cod-end device, has a filtering efficiency of 92%. Possibly, the addition of the cod-end sampler would slightly reduce efficiency.

The major limitation of the IKMT with the cod-end closing device is that contamination of chambers can occur when specimens caught in the mesh of the net during sampling with one chamber are later washed into a subsequent chamber. The design of the sampling program requires that all three chambers fish sequentially for one hour at one depth, which greatly reduces the problem of contamination. The net essentially does not fish while being set with all chambers open (Aron *et al.*, 1964) and specimens that may enter chambers from a previous tow are identifiable by their poor condition and can be eliminated from analysis.

The rectangular midwater trawl 8

The National Institute of Oceanography (NIO), now the Institute of Oceanographic Sciences (IOS), in Great Britain had carried out studies of midwater organisms in the eastern Atlantic for several years using the mouth-closing RMT nets from RRS *Discovery* (Foxton, 1969; Baker *et al.*, 1973).

The sampling program conducted in the eastern North Atlantic by IOS (Currie, Boden & Kampa, 1969) has, since 1968, utilized primarily the rectangular midwater trawls described by Baker *et al.* (1973). The mesh size (bar measure) of the RMT 8 was 4·5 mm throughout its length with a 1·5 m section of 0·75 mm mesh ahead of the cod-end bucket. The area of the mouth opening in fishing configuration was 8·0 m^2. A 1·0 m^2 RMT was rigged on the frame above the RMT 8, but catches from this net are not analysed here. The RMT 8 closing is achieved at the mouth of the net, a design intended to eliminate contamination during set and retrieval. One sample per tow is taken at each depth, rather than three sequential samples. The monitoring system acoustically telemeters information on depth of net, opening-closing events, flow (relative velocity and distance travelled), and temperature.

The opportunity to compare the Ocean Acre program and the IOS sampling techniques and nets arose in 1973 when a sampling survey was conducted in the Ocean Acre area from RRS *Discovery*.

The Engel midwater trawl

The Engel trawl fished during the Ocean Acre program is a very large midwater trawl originally developed for the commercial herring fishery (Schärfe, 1960). It is fished entirely as an open net. The 1400 mesh model of the Engel trawl is somewhat smaller than the standard 1600 mesh EMT net, but its manner of operation is the same as described by Schärfe (1964). The mesh size (bar measure) of the EMT is 101 mm in the wings; it tapers to 38 mm in the cod end. The last 15·2 m of the cod end is lined with a 12 mm-mesh bag. A precise measure of the mouth opening of the EMT is difficult to obtain because the behaviour of these large midwater trawls under tow is not fully understood. Mouth opening can be altered by variations in ship speed, type of doors, diameter of warps and so on. Measurements of 11 m of vertical mouth opening were made on the 1400 mesh EMT during trials prior to the Ocean Acre cruise. It was not possible to take measurements of horizontal spread, but it was estimated to be about twice that of the vertical opening, or 22 m, giving a cross-sectional area of the mouth of 242 m^2 (K. Smith, pers. comm.). The fishing depth was determined by wire angle and recorded by time-depth recorder.

Table I lists the specifications of the three nets.

TABLE I

Mesh size (bar measure) and area of mouth of midwater trawls

Gear	Mesh size		Mouth
	Main body	Cod end	opening (m^2)
3 m IKMT	6·0 mm	3·0 m of 0·75 mm	7·44
RMT 8	4·5 mm	1·5 m of 0·75 mm	8·0
1400 mesh EMT	101 tapered to 38 mm	15·2 m of 12·0 mm	242·0

Sampling procedure

Initially, biologists of the IOS and the Smithsonian Institution planned to conduct a two-ship cruise during the spring of 1973 in order to take simultaneous tows with the IKMT and RMT at identical depths (strata). This type of comparative data would have eliminated seasonal or temporal variability. Unfortunately, the second ship was unavailable so the IKMT could not be used.

The RMT 8 data were accumulated during 13th to 26th March 1973 aboard *Discovery*. The IKMT data were taken during Ocean Acre Cruise 13, 23rd February to 3rd March 1972. So, while the dates of the two collections do not coincide, they do derive from the same season, early spring. Ocean Acre Cruise 6 also occurred in the spring, 25th to 30th April 1969, but fishing effort was only about one-third that of Ocean Acre 13. Combining data from Ocean Acre 6 and 13 will partially reduce the effects of annual fluctuations in populations.

The comparative data for the IKMT versus the EMT were accumulated during consecutive legs of Ocean Acre Cruise 12 from 20th August to 8th September 1971.

Each sampling program required a slightly different technique of trawling. The Ocean Acre sampling strategy called for closing-net samples to be taken at discrete depths (14 depths between 0 and 1500 m) and the range at each depth seldom varied more than 10 m (Gibbs & Roper, 1970; Gibbs *et al.*, 1971). The trawl was set to the desired depth in a non-catching mode, then three sequential one-hour samples in separate chambers were secured from that depth. Sampling speed was 2·5 to 3 knots.

The IOS sampling scheme required the closing-net sampling of 16 depth strata, of varying thickness depending on depth, between 0 and 2000 m. Sampling time was two hours in the 10–1000 m strata and four hours in the 1000–2000 m strata. The RMT was set in a closed mode into the desired depth stratum (e.g. 100 m thick between 100 and 1000 m), opened and fished partly horizontally, partly obliquely for two hours at 2 knots, then closed and retrieved (Baker *et al.*, 1973). During the *Discovery* cruise to the Ocean Acre area the regular IOS sampling strategy was applied, after which a series of tows was made with the RMT 8 fished at discrete depths following the Ocean Acre strategy. We had hoped to make a comparison of the different techniques of sampling, but, unfortunately, foul weather terminated the program early.

The EMT was fished at most of the depths established for the Ocean Acre program (25–1000 m), and fishing time at any given depth varied from half an hour at shallowest depths to two hours at greatest depths. Fishing speed was 1·5 to 2 knots.

Because of the variation in duration of sampling between the types of nets, and because the same nets were fished for varying lengths of time, all captures of cephalopods have been standardized on a catch per effort basis to numbers of specimens captured per hour of trawling. This, at least, makes possible a more meaningful comparison of catches of the same net and between different nets.

RESULTS

All individuals taken by each net (except the EMT) were analysed separately as night-time or day-time captures. Captures made during crepuscular periods, one hour before and one hour after sunrise and sunset, were excluded from the analysis. To facilitate inter-net sample comparison, the water column was divided into contiguous sampling strata similar to those of the IOS sampling procedures, and discrete samples taken by the IKMT and RMT from within any particular stratum were compared.

The following comparisons were made of captures by the 3 m IKMT versus the RMT 8 and the 3 m IKMT versus the EMT 1400: (1) total numbers of species, (2) composition of catch by species, (3) co-occurrence of species, (4) catch rate, (5) size range of specimens by species.

Isaacs-Kidd versus rectangular midwater trawl

Tables II and III present the number of species captured at each depth horizon for day and night, and the average number of specimens captured per hour of trawling at each depth.

Day (Table II). The RMT captured specimens in all 13 depth strata while the IKMT captured specimens in eight of the 12 strata in which it was fished during the day. In ten of the 12 strata co-sampled during the day, the RMT captured a greater number of species than the IKMT. Within the IKMT group the maximum numbers of species were caught in the 51–100 m, 301–400 m, and 401–500 m strata; below 500 m, numbers of species fell off sharply. The numbers of species caught by the RMT, however, remained relatively high throughout the water column, with a maximum of 14 species captured in the 101–200 m stratum. The total number of species captured by both nets shows a maximum number of species (13–14) in the day-time in the 51–200 m strata; below 200 m numbers are nearly constant (6-8 species) with reduced numbers at

TABLE II

IKMT and RMT captures by species and catch rate during the day

	IKMT					RMT					
	OA 6		OA 13		IKMT Total	A-A		A		RMT Total	No. of species in both nets
Depth (m)	No. spp.	Av. no./hr	No. spp.	Av. no./hr	no. spp.	No. spp.	Av. no./hr	No. spp.	Av. no./hr	no. spp.	
12–25	—	—	—	—	—	—	—	6	0·7	6	6
26–50	—	—	2	15·2	2	—	—	4	9·7	4	4
51–100	9	2·2	2	3·2	9	—	—	6	6·0	6	13
101–200	—	—	0	0	0	—	—	14	1·25	14	14
201–300	0	0	—	—	0	—	—	4	0·6	4	4
301–400	3	1·7	1	2·0	4	—	—	5	1·3	5	8
401–500	0	0	5	3·4	5	—	—	2	4·0	2	6
501–600	0	0	—	—	0	1	0·5	2	9·5	3	3
601–700	—	—	3	1·8	3	—	—	5	1·9	5	7
701–800	0	0	2	0·8	2	—	—	5	0·6	5	6
801–900	—	—	1	1·0	1	5	0·7	2	0·5	6	6
901–1000	0	0	—	—	0	5	0·7	2	1·0	6	6
1001–1250	—	—	2	1·0	2	4	0·3	5	0·5	7	7
(lumped) 0–100	9	2·2	3	9·1		—	—	10	4·6		13

Number of species, average number of specimens/hr of trawling, total number of species/net, grand total number of species for both nets.
— Indicates no tow made at that depth.
0 Indicates no catch in the tow at that depth.
OA 6, OA 13: Ocean Acre Cruise 6 and 13 respectively.
A-A: RMT tows made under Ocean Acre sampling regime.
A: RMT tows made under IOS sampling regime.

201–300 m and 501–600 m (Fig. 1). During the day the IKMT caught a total of 18 different species and the RMT caught 37 species, with seven species common to both nets.

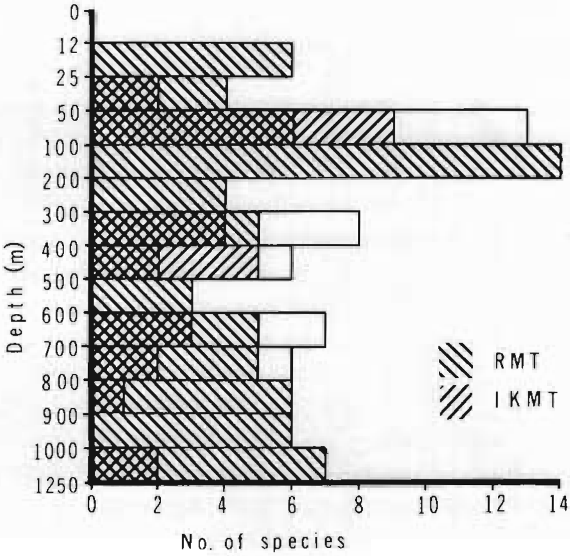

FIG. 1. Number of species captured by IKMT, RMT, and both trawls combined during the day. Total numbers of species represented by open area.

The catch rate of the IKMT, in terms of the average number of specimens per species per hour, exceeded that of the RMT in four of the eight strata in which both trawls caught specimens; catch rates were nearly equal in two horizons, and those of the RMT exceeded the IKMT at two horizons.

Night (Table III). The IKMT captured specimens in ten of the 11 strata in which it fished and the RMT caught specimens in all the 13 depth strata. The nets co-sampled in 11 strata; the RMT captured more species in seven of the strata, the IKMT caught more in two strata, and catches were equal in two strata. The IKMT data showed species diversity maxima, 12 and 16, in the 51–100 m and the 101–200 m horizons, respectively; between 201 and 600 m a reduced but fairly constant diversity of four to six species occurred. In the upper 300 m the RMT captured between eight and ten species, except at 101–200 m where a maximum catch of 16 species was recorded. Species decreased irregularly below 301 m. The total number of species captured by both nets was high (12–21) in

TABLE III

IKMT and RMT captures by species and catch rate during the night

	IKMT					RMT					
	OA 6		OA 13			A-A		A			
Depth (m)	No. spp.	Av. no./hr	No. spp.	Av. no./hr	IKMT Total no. spp.	No. spp.	Av. no./hr	No. spp.	Av. no./hr	RMT Total no. spp.	No. of species in both nets
10–25	—	—	7	16·8	7	—	—	8	11·0	8	12
26–50	4	1·4	4	9·1	8	8	2·6	5	13·3	10	15
51–100	—	—	12	2·13	12	5	6·2	7	12·1	8	13
101–200	11	1·6	12	1·0	16	11	1·7	12	2·8	16	21
201–300	3	1·3	5	2·4	6	—	—	9	1·2	9	12
301–400	—	—	5	2·3	5	—	—	7	1·1	7	10
401–500	—	—	4	1·0	4	4	1·2	3	0·7	6	9
501–600	—	—	5	1·1	5	—	—	4	0·7	4	8
601–700	—	—	—	—	—	—	—	2	2·0	2	2
701–800	—	—	2	1·3	2	0	0	5	0·7	5	5
801–900	—	—	—	—	—	—	—	1	0·5	1	1
901–1000	—	—	1	1·0	1	—	—	1	0·5	1	2
1000–1250	0	0	0	0	0	1	0·3	2	1·1	3	3
(lumped) 0–100	—	—	15	8·1		11	4·0	11	12·48		22

Number of species, average number of specimens/hr of trawling, total number of species/net, grand total number of species for both nets.
— Indicates no tow made at that depth.
0 Indicates no catch in the tow at that depth.
OA 6, OA 13: Ocean Acre Cruise 6 and 13 respectively.
A-A: RMT tows made under Ocean Acre sampling regime.
A: RMT tows made under IOS sampling regime.

the upper 300 m, peaking at 21 species in the 101–200 m stratum. Below 301 m total species diversity decreased (Fig. 2). At night the IKMT captured 30 different species while the RMT caught 28 species with 15 species captured in common.

The catch rate of the IKMT exceeded that of the RMT in seven of the 11 co-sampled strata at night; the RMT had greater catch rates at four strata.

Figures 1 and 2 also present a vivid demonstration of the diel vertical migrations which many species undertake.

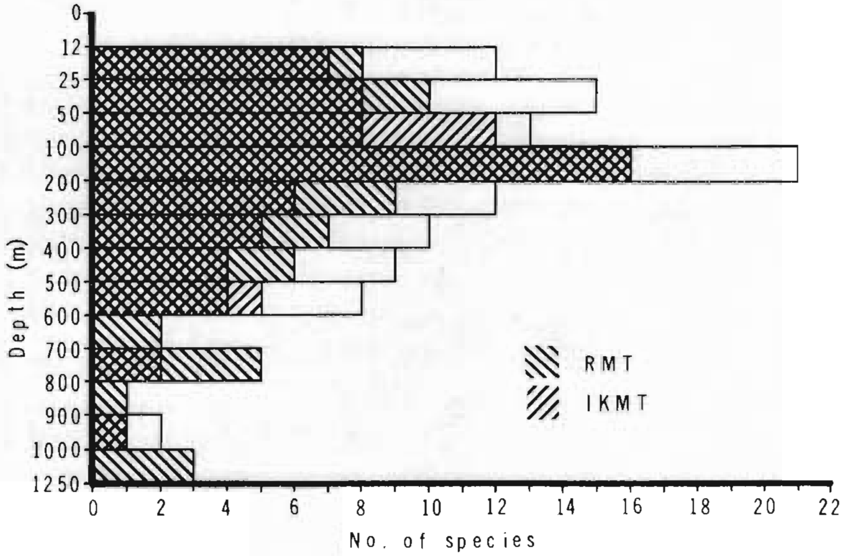

FIG. 2. Number of species captures by IKMT, RMT, and both trawls combined during the night. Total numbers of species represented by open area.

A comparison was made of the species composition found in the two nets. During the comparative cruises a total of 50 species was captured, and 22 species were common to both the IKMT and the RMT. Table IV lists the co-occurring species with number of specimens, size range and mean for each net, and the per cent difference of number of specimens and average size between the captures of the IKMT and the RMT. Size is recorded in mm as mantle length (ML). Number of specimens is listed to provide an indication of the sample size for the calculation of mean mantle lengths; it is not indicative of the catch rates of the nets because effort is not taken into account.

TABLE IV

Co-occurring species in IKMT and RMT

Species	IKMT		RMT		% Difference	
	No. of specimens	ML	No. of specimens	ML	No.	ML
1. *Selenoteuthis scintillans*	4	10-*13*-17	3	12-*15*-17	−25	+15
2. *Abraliopsis pfefferi*	5	6-*14*-22	21	4-*12*-34	+320	−14
3. *Pyroteuthis margaritifera*	66	4-*15*-60	47	2-*6*-15	−29	−60
4. *Pterygioteuthis giardi*	15	5-*13*-19	45	3-*11*-18	+200	−15
5. *Octopoteuthis danae*	1	*17*	1	*16*	0	−6
6. *Octopoteuthis* sp.	12	7-*10*-13	3	2-*5*-7	−75	−50
7. *Onychoteuthis banksi*	4	13-*16*-20	14	2-*9*-18	+250	−44
8. *Histioteuthis dofleini*	1	*23*	10	4-*19*-115	+900	−17
9. *Histioteuthis corona*	1	*12*	2	9-*11*-13	+100	−8
10. *Ctenopteryx sicula*	12	4-*10*-16	15	2-*7*-21	+25	−30
11. *Brachioteuthis riisei*	13	10-*15*-27	15	5-*10*-20	+15	−33
12. *Ommastrephes* sp.	7	4-*14*-27	2	4-*5*-6	−71	−64
13. *Mastigoteuthis magna*	1	*23*	6	10-*20*-35	+900	−13
14. *Mastigoteuthis* sp.	2	21-*21·5*-22	16	4-*15*-45	+700	−30
15. *Leachia cyclura*	609	5-*23*-50	503	8-*25*-55	−17	+9
16. *Bathothauma lyromma*	10	5-*13*-21	8	4-*6*-10	−20	−54
17. *Helicocranchia* sp.	9	6-*14*-60	212	2-*10*-55	+2256	−29
18. *Egea inermis*	3	8-*13*-17	1	*46*	−67	+254
19. *Eledonella pygmaea*	10	5-*11*-26	32	3-*12*-21	+220	+9
20. *Vitreledonella richardi*	3	10-*10·6*-11	1	*11*	−67	+4
21. *Argonauta argo*	1	*9*	2	7-*8*-9	+100	−11
22. *Alloposus mollis*	2	5-*6·5*-8	1	*3*	−50	−54

Number of specimens, minimum-*mean*-maximum size by mantle length (ML) in mm, per cent difference in numbers and mantle length.

In the per cent difference columns, a positive value indicates that the RMT caught larger average size or greater numbers of specimens and a negative value indicates that the IKMT caught more or larger specimens. Occasionally one net provided the largest average size of a species, but the other net will have caught the largest specimen, for example, *Abraliopsis pfefferi*. The tendency exists for the IKMT to catch specimens of a slightly larger mean mantle length than the RMT catches. Large differences in mean size often occurred in species in which very few specimens were caught, for example, *Alloposus mollis*, or where there was a significant difference between the numbers of specimens caught, as in *Octopoteuthis* sp. In the case of *Egea inermis*, only one specimen was caught in the RMT, but it was much larger than any of the three caught in the IKMT. The difference in catches of *Ommastrephes* sp. may indicate an ability of the IKMT to catch faster swimming forms, as it caught more and significantly larger specimens than did the RMT. Such differences could be a reflection of the small sample size rather than of major differences between the nets.

Where sample size is large enough for both nets, specimens of the co-occurring species that occur in reasonable numbers generally do not exhibit a wide disparity in mean or maximum mantle length. Specimens of the well represented *Pyroteuthis margaritifera* caught in the IKMT, however, are notably larger in average mantle length and maximum mantle length than the specimens from the RMT.

An examination of the minimum size of specimens indicates that the RMT caught smaller individuals in 17 of the 22 species. In many species the difference was of the same magnitude as occurs for differences in maximum size. The difference in mesh size between the two nets is probably sufficient to account for this phenomenon, as the RMT has a mesh size of 4·5 mm while that of the IKMT is 6·0 mm. The mesh size of the cod-end liners of both nets is 0·75 mm.

Several techniques for measuring co-occurrence exist, one of which is the Index of Similarity, calculated from the formula:

$$S = \frac{2C}{A+B}$$

where A is the number of species in the IKMT (32), B is the number of species in the RMT (40), and C is the number of species common to both trawls (22). In this case $S = 0{\cdot}61$. If the 0·85 level is considered the limit of similarity, an index of similarity of 0·61 indicates that, so far as species composition is concerned, the two nets are relatively dissimilar. In order for the nets to be regarded as similar, at least 31 co-occurring species would be required. Another comparison that can be applied to measure the similarity of the two nets in relation to species composition is Jaccard's Coefficient of Community. This measure is expressed by the formula

$$cc = \frac{c}{a+b-c} \times 100$$

where a and b are the total number of species in the IKMT and RMT, respectively, and c is the number of co-occurring species. Therefore,

$$cc = \frac{22}{32+40-22} \times 100 = 44\%,$$

on a scale where 100% represents identical species representation and 0 corresponds to no relationship. To achieve a level of 85%, a reasonable limit of similarity, 33 species would have to co-occur in the two nets. The coefficient of community of 44% also indicates that the IKMT and the RMT are relatively dissimilar in species composition.

Of the 50 species captured during the study period, 22 were co-captured in both nets. Ten species were captured solely by the IKMT, and 18 species were captured only by the RMT (Table V). Most of these species were represented by low catch numbers; only five of these 28 species consisted of more than five specimens (6, 6, 8, 10, 48).

The catch rates and size ranges of co-occurring species within each depth stratum have been compared. During the day (Table VI), for example, *Leachia cyclura* was co-captured in the 26–50 m stratum at a nearly equivalent catch rate of 28·9 specimens per hour for the IKMT and 32·5 specimens per hour for the RMT. The size ranges and means also were similar. At 51–100 m, however, a significant difference occurs in that the RMT caught many more specimens per hour and of somewhat larger maximum size than the IKMT, although the mean size was about the same as that of the Ocean Acre 6 sample. *Pyroteuthis margaritifera* co-occurred at the 301–400 m and 401–500 m strata, where the RMT had a

TABLE V

Non-co-occurring species in IKMT and RMT

Species captured by IKMT but not RMT	No. of speci-mens	ML	Species captured by RMT but not IKMT	No. of speci-mens	ML
1. *Heteroteuthis dispar*	1	*19*	1. *Octopoteuthis sicula*	8	3-*8*-15
2. *Lampadioteuthis megaleia*	6	5-*11*-19	2. *Onykia caribaea*	4	2-*4*-6
3. *Abralia redfieldi*	2	15-*17*-19	3. *Discoteuthis laciniosa*	1	*13*
4. *Taningia danae*	2	8-*8*-8	4. *Lepidoteuthis grimaldi*	4	16-*23*-27
5. *Tetronychoteuthis dussumieri*	1	*21*	5. *Histioteuthis meleagroteuthis*	2	7-*7·5*-8
6. *Brachioteuthis* sp.	5	8-*9*-10	6. *Histioteuthis* sp.	3	4-*4*-5
7. *Taonius pavo*	10	13-*23*-47	7. *Neoteuthis* sp.	1	*11*
8. *Megalocranchia megalops*	1	*8*	8. *Bathyteuthis abyssicola*	6	2-*14*-40
9. *Ocythoe tuberculata*	1	*6*	9. *Brachioteuthis beani?*	1	*4*
10. Octopod	1	*7*	10. *Chiroteuthis veranyi*	3	40-*48*-63
			11. *Mastigoteuthis hjorti*	1	*20*
			12. *Grimalditeuthis bomplandi*	1	*55*
			13. *Joubiniteuthis portieri*	1	*5*
			14. *Galiteuthis* sp.	48	5-*19*-43
			15. *Egea inermis*	5	7-*12*-16
			16. *Tremoctopus violaceus*	2	6-*7·5*-9
			17. *Scaeurgus unicirrhus*	1	*11*
			18. *Vampyroteuthis infernalis*	4	10-*19*-30

Number of specimens, minimum-*mean*-maximum size by mantle length (ML) in mm.

TABLE VI

Co-occurring species in IKMT and RMT during the day by depth stratum

		No./hr				Size range			
Depth, (m)	Species	OA 6 IKMT	OA 13 IKMT	A-A RMT	A RMT	OA 6 IKMT	OA 13 IKMT	A-A RMT	A RMT
26-50	*B. riisei*	—	1·4	—	2·0	—	12-*12·5*-13	—	14-*17*-20
	L. cyclura	—	28·9	—	32·5	—	10-*21*-35	—	10-*22*-37
51–100	*L. cyclura*	6·3	5·4	—	42·5	25-*38*-47	11-*22*-37	—	19-*34*-55
	Octopoteuthis sp.	3·0	0	—	1·5	8-*9*-10	0	—	7-*10*-15
	Ommastrephes sp.	1·8	1·0	—	0	*27*	*21*	—	0
301–400	*P. margaritifera*	2·0	0	—	3·5	10-*11*-13	0	—	4-*5*-6
401–500	*P. margaritifera*	0	5·2	—	7·5	0	6-*15*-24	—	2-*6*-11
601–700	*L. cyclura*	—	3·0	—	4·0	—	12-*26*-34	—	31-*36*-45
701–800	*E. pygmaea*	0	0·8	—	0·5	0	7-*8*-9	—	*4*
801–900	*Mastigoteuthis* sp.	—	1·0	0	0·5	—	*22*	0	*20*
1000–1250	*E. pygmaea*	—	0·9	0·3	1·0	—	18-*22*-26	13-*14*-15	15-*16*-19
	Mastigoteuthis sp.	—	1·0	0	0·2	—	*21*	0	*45*

Total number of specimens captured/hr of trawling, size range of mantle length (ML) in mm, as minimum-*mean*-maximum.
— Indicates no tow made at that depth.
0 Indicates no catch in the tow at that depth.
OA 6, OA 13: Ocean Acre Cruise 6 and 13 respectively.
A-A: RMT tows made under Ocean Acre sampling regime.
A: RMT tows made under IOS sampling regime.

superior rate of capture. The differences in sizes were marked, however, in that the mean and maximum sizes captured by the IKMT were twice those of the RMT, and the minimum sizes captured by the RMT were considerably smaller than those of the IKMT. In general the RMT had a greater catch rate than the IKMT, especially at depths shallower than 700 m, but the differences for the most part were not large. No firm pattern of difference in size ranges occurs between nets, other than for *P. margaritifera.*

At night a larger number of species co-occur (Table VII) than during the day, especially in the 51–100 m and the 101–200 m strata. Also, the catch rates of both nets are markedly higher. *Pyroteuthis margaritifera,* caught in four of the upper five strata, again demonstrates a consistently larger size of specimens in the IKMT than the RMT, and in three of the four captures the IKMT caught a notably higher number of specimens per hour. Save for the 10–25 m stratum, the highest catch rates in the upper 200 m were recorded by the RMT (14 of 19 co-occurring species). Below 201 m seven of the nine species were caught at a greater number per hour by the IKMT than the RMT. The depth range below 201 m also corresponds to markedly reduced capture rates by both nets.

The general trend, as in other comparisons, is for the IKMT to catch a larger mean size of specimens per species than the RMT, but this trend is reversed in *Leachia cyclura. L. cyclura* was present in eight of the nine horizons in which co-occurring species were recorded, and in nearly every case its minimum, mean, and maximum sizes in the RMT exceeded those of specimens in the IKMT.

Isaacs-Kidd versus Engel trawl

The comparative tows of the IKMT versus the EMT were made consecutively on Ocean Acre Cruise 12 in the same depth strata over a three-week period during August–September, 1971. Since the EMT was fished as an open net no discrete depth comparisons were possible, and neither were there any day/night comparisons.

During Ocean Acre 12 a total of 54 species was captured, 20 of which were co-occurring species in the IKMT and the EMT (Table VIII). The EMT fished only about half the number of hours (55%) of the total at depth trawling time of the IKMT. So, while Table VIII does not show effort as specimens per hour *per se,* it should be noted that the IKMT catches do represent about twice the effort of the EMT. The extreme difference in catches both in terms of

TABLE VII

Co-occurring species in IKMT and RMT during the night by depth stratum

Depth (m)	Species	No./hr				Size range			
		OA 6 IKMT	OA 13 IKMT	A-A RMT	A RMT	OA 6 IKMT	OA 13 IKMT	A-A RMT	A RMT
10–25	*L. cyclura*	—	106·0	—	89·0	—	7-*15*-29	—	12-*21*-37
	P. margaritifera	—	5·0	—	1·0	—	10-*13*-20	—	*4*
	B. riisei	—	2·5	—	1·0	—	14-*16*-18	—	*5*
25–50	*P. giardi*	2·0	0	1·5	4·5	5-*7*-11	0	8-*10*-12	6-*10*-15
	B. riisei	0	1·0	3·0	0·5	0	*12*	9-*9·5*-10	*20*
	L. cyclura	0	33·2	10·5	59·5	0	5-*18*-30	10-*13*-15	12-*24*-40
51–100	*P. giardi*	—	1·6	2·5	11·5	—	8-*13*-17	8-*13*-18	3-*9*-15
	P. margaritifera	—	1·3	0·5	5·0	—	4-*18*-28	*3*	2-*4*-6
	L. cyclura	—	11·6	25·0	11·0	—	9-*17*-36	8-*19*-22	16-*21*-30
	Helicocranchia sp.	—	1·6	0	54·0	—	6-*9*-11	0	3-*9*-55
	A. pfefferi	—	1·0	2·5	2·5	—	*6*	15-*16*-18	7-*22*-34
	O. banksi	—	1·0	0	0·5	—	*13*	0	*5*
	C. sicula	—	1·0	0	0·5	—	*16*	0	*2*
101–200	*P. margaritifera*	7·0	1·0	1·0	3·5	8-*12*-20	14-*18*-26	10-*11*-12	2-*8*-15
	C. sicula	1·5	1·0	0	2·5	4-*6*-10	*10*	0	4-*8*-21
	Mastigoteuthis sp.	1·0	0·4	0·5	2·0	6-*15*-25	*23*	*10*	4-*7*-12
	L. cyclura	1·4	1·4	2·5	5·0	24-*29*-45	21-*27*-39	22-*25*-30	14-*29*-44
	Helicocranchia sp.	1·0	1·2	9·0	14·0	13-*17*-21	13-*20*-30	4-*11*-20	4-*10*-20
	Octopoteuthis sp.	1·0	1·0	1·5	0·5	*7*	*10*	*3-4-5*	*5*
	O. banksi	1·0	0·8	2·0	0·5	*14*	*20*	11-*15*-18	*5*
	B. riisei	1·0	0	0·5	0	*27*	0	*7*	0
	B. lyromma	0	1·3	1·0	1·0	0	5-*12*-22	6-*6·5*-7	4-*4*-4

201–300	*L. cyclura*	1·5	2·0	—	0	33-*42*-48	26-*32*-36	—	0
	V. richardi	1·0	1·0	—	0	*10*	11-*11*-11	—	0
	P. margarilifera	0	3·0	—	0·5	0	22-*39*-60	—	*12*
	E. pygmaea	0	3·0	—	0·5	0	6-7-8	—	*5*
301–400	*B. lyromma*	0	3·0	—	0·5	0	8-*11*-15	—	*10*
	H. dofleini	—	3·0	—	1·0	—	*23*	—	4-*5*-6
401–500	*L. cyclura*	—	5·2	—	4·0	—	17-*22*-32	—	4-*24*-40
	L. cyclura	—	1·0	3·0	0	—	8-*18*-25	19-*26*-50	0
501–600	*H. dofleini*	—	0	1·0	1·0	—	0	4-*8*-12	6-*6·5*-7
701-800	*L. cyclura*	—	1·5	—	1·0	—	15-*19*-23	—	30-*30*-30
	L. cyclura	—	1·6	0	0·5	—	14-*22*-35	0	*45*
	E. pygmaea	—	1·0	0	1·5	—	*9*	0	4-*6*-8

Total number of specimens captured/hr of trawling, size range of mantle length (ML) in mm, as minimum-*mean*-maximum.
— Indicates no tow made at that depth.
0 Indicates no catch in the tow at that depth.
OA 6, OA 13: Ocean Acre Cruise 6 and 13 respectively.
A-A: RMT tows made under Ocean Acre sampling regime.
A: RMT tows made under IOS sampling regime.

TABLE VIII

Co-occurring species in IKMT and EMT, Ocean Acre 12

Species	IKMT		EMT		% Difference	
	No. of specimens	ML	No. of specimens	ML	No.	ML
1. *Selenoteuthis scintillans*	5	8-*11*-14	23	11-*29*-45	360	164
2. *Abraliopsis pfefferi*	11	5-*18*-39	239	12-*25*-38	2073	39
3. *Abralia redfieldi*	1	*8*	158	18-*24*-38	15 700	200
4. *Thelidioteuthis alessandrinii*	5	6-*8*-10	7	18-*22*-31	40	175
5. *Pyroteuthis margaritifera*	44	4-*12*-41	199	10-*24*-49	352	100
6. *Pterygioteuthis giardi*	12	9-*13*-17	17	14-*16*-20	42	23
7. *Octopoteuthis danae*	1	*27*	3	34-*115*-159	200	326
8. *Onychoteuthis banksi*	25	5-*9*-21	64	12-*26*-45	156	189
9. *Discoteuthis laciniosa*	1	*42*	3	52-*82*-134	200	95
10. *Histioteuthis dofleini*	7	8-*41*-176	40	8-*41*-125	471	0
11. *Brachioteuthis riisei*	2	13-*16*-18	4	40-*54*-68	100	237
12. *Mastigoteuthis magna*	6	20-*29*-50	14	27-*77*-151	133	166
13. *Taonius pavo*	2	39-*64*-88	33	55-*100*-231	1550	56
14. *Bathothauma lyromma*	5	6-*35*-95	29	12-*74*-130	480	111
15. *Helicocranchia pfefferi*	52	6-*13*-34	39	13-*27*-49	−25	108
16. *Egea inermis*	43	5-*24*-43	71	12-*33*-425	65	37
17. *Eledonella pygmaea*	4	13-*20*-32	102	13-*28*-43	2450	40
18. *Vitreledonella richardi*	2	6-*11*-15	1	*57*	−100	418
19. *Tremoctopus violaceus*	3	6-*7*-8	1	*12*	−200	71
20. *Argonauta argo*	1	*7*	1	*10*	—	43

Number of specimens, minimum-*mean*-maximum size by mantle length (ML) in mm, percentage difference in numbers and ML.

numbers of specimens captured per hour per unit area of mouth-opening and of size ranges is readily apparent. The difference in numbers captured, however, is not so great in the smaller species, such as *Pterygioteuthis giardi*, and with three small and/or "rare" species the IKMT caught more specimens than the EMT, for example, *Vitreledonella richardi*. The EMT caught considerably larger specimens in 19 of the 20 species, the only exception being *Histioteuthis dofleini*. Otherwise specimens ranged from slightly larger, for example, *Pterygioteuthis giardi*, to several times larger, as in *Octopoteuthis danae*, and up to nearly ten times larger in maximum size, as in *Egea inermis*.

An index of similarity of 0·54 and a Jaccard's coefficient of community value of 37% for co-occurring species between the IKMT and the EMT indicate a predictable dissimilarity.

The EMT captured 25 species that were not captured by the IKMT, while the IKMT caught nine species not taken by the EMT (Table IX). The species caught in the IKMT generally were represented by quite small specimens, and only two of the nine species were represented by more than two specimens. Most species taken by the EMT, on the other hand, were large and some of them, for example, *Ommastrephes bartrami* and *Todarodes sagittatus*, represent the largest specimens ever taken in the Ocean Acre program. Numbers of specimens range from one to nearly 100. *Hyaloteuthis pelagica* is a very rarely caught squid, represented by only a few records in the literature. The EMT captured 96 specimens which ranged from 9 to 93 mm in mantle length. These captures exceed the numbers (fewer than 20) and maximum size (71 mm mantle length) of all previously recorded specimens (Clarke, 1966).

DISCUSSION

A comparison of captures of cephalopods was conducted using three different midwater trawls, the 3 m IKMT, the RMT 8, both closing nets, and the 1400 mesh EMT, a non-closing net. Although the data are somewhat limited, they do indicate that the three nets sample cephalopods differently. As a result they depict different aspects of ecological communities, because of differences in design, techniques of fishing, and so on.

In the IKMT versus RMT comparison, 50 species were captured in all, 40 in the RMT and 32 in the IKMT; 22 species co-occurred. Analysis of the species composition of both nets based on co-occurrence of species indicates that the captures of the two nets are not highly similar in species content. The index of

TABLE IX

Non-co-occurring species in IKMT and EMT, Ocean Acre 12

Species captured by EMT but not by IKMT	No. of specimens	ML	Species captured by IKMT but not by EMT	No. of specimens	ML
1. *Enoploteuthis leptura*	2	26-*44*-63	1. *Spirula spirula*	1	*18*
2. *Enoploteuthis anapsis*	27	12-*48*-93	2. *Octopoteuthis* sp.	2	8-*8·5*-9
3. *Octopoteuthis sicula*	8	33-*115*-167	3. *Bathyteuthis abyssicola*	1	*12*
4. *Taningia danae*	1	*26*	4. *Ommastrephes* sp.	4	5-*6*-8
5. *Onykia caribaea*	1	*9*	5. *Grimalditeuthis bomplandi*	2	45-*53*-61
6. *Cycloteuthis sirventi*	1	*134*	6. *Liocranchia reinhardti*	5	7-*8*-12
7. *Tetronychoteuthis dussumieri*	2	44-*72*-100	7. *Leachia* sp.	1	*55*
8. *Histioteuthis meleagroteuthis*	29	27-*50*-109	8. *Megalocranchia megalops*	2	8-*9·5*-11
9. *Histioteuthis corona*	7	22-*42*-56	9. *Thysanoteuthis rhombus*	1	*4*
10. *Neoteuthis* sp.	2	20-*30*-40			
11. *Ctenopteryx sicula*	31	12-*26*-45			
12. *Ommastrephes bartrami*	3	310-*380*-518			
13. *Ornithoteuthis antillarum*	2	188-*192*-196			
14. *Hyaloteuthis pelagica*	96	9-*49*-93			
15. *Todarodes sagittatus*	1	*341*			
16. *Chiroteuthis veranyi*	3	75-*79*-81			
17. *Chiroteuthis* sp. A.	3	107-*116*-133			
18. *Chiroteuthis* sp. C.	5	39-*59*-83			
19. *Chiroteuthis* sp. B.	1	*84*			
20. *Mastigoteuthis hjorti*	12	27-*66*-181			
21. *Mastigoteuthis grimaldi*	2	?			
22. *Cranchia scabra*	1	*30*			
23. *Eledonella* sp. A.	5	33-*36*-44			
24. *Vampyroteuthis infernalis*	1	*28*			
25. Octopod sp. A.	7	13-*14*-15			

Number of specimens, minimum-*mean*-maximum size by mantle length (ML) in mm.

similarity = 0·61 and the coefficient of community = 44%. Caution should be applied in interpreting these results, however. The co-occurring species are the most commonly caught species, and conversely, the non-co-occurring species tend to be caught much more rarely. Insufficient sampling time may be a factor. Also, since the IKMT/RMT comparative tows were taken one year or more apart, even though they occurred during the same season, some differences may be expected due to annual fluctuations of occurrence and abundance of species. In the total Ocean Acre program the IKMT has caught all the species that are recorded only from the RMT in this study.

The IKMT captured 821 specimens in 112·6 hr of trawling for a catch per effort measure of 7·29 specimens/hr. The RMT captured 1057 specimens in 83·0 hr of trawling for a catch rate of 12·73 specimens/hr. In order to determine the relationships of the two catch rates, the catch per unit area of the mouth opening of each net has been calculated. The mouth area of the 3 m IKMT is 7·44 m^2, so the catch per area is:

$$\frac{7{\cdot}29\ \text{specimens/hr}}{7{\cdot}44\ \text{m}^2} = 0{\cdot}89\ \text{specimens/hr/m}^2.$$

The area of the mouth of the RMT 8 is 8 m^2 divided into the catch rate of 12·73 specimens/hr yields a value of 1·59 specimens/hr/m^2. In other words, the differences in the catch rates are not due to the differences in the area of the mouth opening of the nets. The RMT does catch more specimens per unit effort than the IKMT. Several explanations are possible. For example, the smaller mesh size of the RMT may be more efficient at catching larger numbers of smaller specimens, or the escape rate may be higher because of the bridle arrangement on the IKMT.

The IKMT and RMT differ somewhat in the size of specimens captured. The IKMT tends to catch animals of slightly larger mean mantle length, while the RMT catches markedly smaller minimum length specimens within species. These differences possibly are attributable to the smaller mesh size of the RMT net, 4·5 mm versus 6·0 mm.

The RMT caught a higher number of species during the day than the IKMT, but at night the IKMT caught slightly more than the RMT. No pattern of catch rates by day or night was evident between the two nets.

Finally, individual species differences seem to occur between nets. Specimens of *Pyroteuthis margaritifera*, for instance, were consistently larger and more frequently caught in the IKMT than in the RMT. *Leachia cyclura* was consistently larger in minimum, mean, and maximum size in the RMT than in the IKMT, a specific reversal of the general trend.

Studies of the IKMT versus the EMT had the advantage that the comparative tows were taken sequentially on the same cruise, but are limited because the EMT could be fished only as an open net. A total of 54 species was captured during the comparative tows, and 20 species co-occurred in both nets. The IKMT caught a total of 29 species, while the EMT captured 45 species. Little doubt exists as to the ability of the EMT to make superior captures in terms of numbers of species, numbers of specimens, and size of specimens.

The index of similarity of 0·54 and the coefficient of community of 37% indicate the relatively dissimilar catches in terms of species composition. The cautions mentioned in the discussion of the IKMT and RMT comparison may apply here, as well, although certainly to a lesser degree, because the EMT did catch some species that had not previously been recorded from the Ocean Acre program.

The EMT caught 1306 specimens in 68·83 hr of trawling for a catch rate of 18·9 specimens/hr, while the IKMT caught 250 specimens in 122·38 hr, or 2·0 specimens/hr. The value of catch rate by mouth area for the EMT is 0·78 specimens/hr/m^2 and that of the IKMT is 0·27 specimens/hr/m^2. Size range differences within species varied from specimens of about equal length, up to ten times larger in the EMT than in the IKMT.

As would be expected, a greater dissimilarity exists between the IKMT and the EMT than between the IKMT and the RMT in terms of species composition, numbers, and sizes of specimens and catch rates.

An interesting comparison is noted between the results ot this study and the work of Clarke & Lu (1974) who reported on the vertical distribution of cephalopods in the eastern Atlantic at 30°N 23°W. Information extracted from their data indicates that 28 species were captured in the IKMT and 27 species were caught in the RMT for a total of 38 species, with 17 co-occurring species. These figures were tested for similarity with the following results:

Index of Similarity = 0·62
Coefficient of Community = 45%.

The measurements of similarity are nearly identical with those of the current study, i.e. 0·61 and 44%, indicating that a certain degree of predictability is justified when these two types of nets are fished in the same area.

The IKMT and the RMT used in the study reported by Clarke & Lu (1974) at 30°N 23°W caught a combined total of 618 specimens in 160 hr of trawling for an average catch rate of 3·86 specimens/hr. The same types of nets in the Ocean Acre area off Bermuda (32°N 64°W) captured a combined total of 1878 specimens in 195 hr of sampling for an average catch rate of 9·63 specimens/hr. Based on the two IKMT/RMT studies, a greater number of species occurs in the Bermuda area than in the eastern Atlantic at a similar latitude (50 to 38°), and a greater catch rate is recorded. These data indicate a greater species diversity and a greater relative abundance of cephalopods in the waters east of Bermuda.

Certain limitations occur that may affect the results of this comparative study of midwater trawls as many variables exist in the sampling of nektonic organisms. The attempts at reducing the variables in this study represent a reasonable beginning but fall short of the most desirable conditions. Ideally, we would like to have simultaneous tows of two types of gear from two vessels running parallel courses with nets fishing at identical depths and straining identical quantities of water. This is seldom, if ever, possible. Even then problems of the patchiness in the distributions of midwater organisms must be taken into account. A further limitation to thoroughly assessing the community structure of oceanic cephalopods is that the systematics and life histories of many families are inadequately known. Sufficiently thorough sampling often is a limitation. Both the IOS and the Ocean Acre studies were designed to overcome this problem. The sampling strategies of both the Ocean Acre program and the IOS require 13 tows each for day-time and night-time sampling at 0–1250 m, which should be adequate for the most abundantly captured species, at least. The comparison of samples from the same season or from sequential tows and the standardization of closing-net captures for sampling effort help to reduce the aforementioned limitations.

We know from the experience of this work and from previous work, including studies of sperm whale stomach contents (see Clarke, his chapter, this volume), that we are still not sampling the total pelagic cephalopod fauna. Any net used exclusively gives only a truncated view of the populations of cephalopods. Several different nets are required for a complete assessment.

The present comparative study of midwater trawl captures represents the first attempt at a quantitative analysis of the midwater cephalopod fauna based on standardized capture data. Such comparisons are necessary if we are to interpret the results of various midwater trawl studies, and ultimately, if we are to understand the communities of pelagic cephalopods.

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