

AVOIDANCE OF TOWED NETS BY THE EUPHAUSIID *NEMATOSCELIS MEGALOPS*¹

P. H. WIEBE,² S. H. BOYD,² B. M. DAVIS,² AND J. L. COX³

ABSTRACT

Avoidance of towed nets by the common oceanic euphausiid crustacean *Nematoscelis megalops* was studied by comparing aspects of its sampling distribution as revealed by day and night catches of two nets of different size, one with a 1 m² mouth opening and one with a 10 m² opening. Both nets yield essentially the same pattern in vertical distribution. Paired tows yield a highly significant agreement in nighttime abundance estimates, but do not give comparable daytime estimates. Night catches, especially with the smaller net, exceed day catches, an effect which is interpreted as resulting from greater avoidance during the day. Comparisons between nets show that neither size net has a superior catch rate, day or night. No particular size group of the species is caught with greater efficiency by either net. When *N. megalops*' center of distribution is shallower, differences between day and night catches can be substantially enhanced.

Application of Barkley's avoidance theory indicates that the potential advantage of greater mouth area of the larger net is effectively cancelled by individuals reacting to the approach of the net at a greater distance. Other theoretical predictions which depend upon the assumption of increasing escape velocities as a function of body size are not corroborated by the field data. Thus, field population size-frequency distributions are probably not materially affected by avoidance.

The evidence suggests that *N. megalops* uses vision to detect the net approach. Net contrast with the background due to down-welling light during the day and bioluminescence produced in and around the net both day and night appear to be the most likely stimuli. Future efforts to reduce net avoidance by species like *N. megalops* must focus on reduction of these signals.

Avoidance of capture by towed nets is a major source of underestimation bias associated with zooplankton abundance measurements (Clutter and Anraku 1968; Wiebe and Holland 1968; Wiebe 1971). This factor is perhaps the most important determinant of the accuracy of abundance estimates for some of the larger zooplankton species. Patchiness of zooplankton may cause large differences between successive tows taken at a single station (Wiebe 1971; Wiebe et al. 1973), but the error induced by this factor is not comparable with avoidance error, since patchiness "error" is essentially unbiased. The precision of the estimate of abundance for a particular station location will improve with greater sample numbers, but avoidance error will persist as an underestimation bias. Since patchiness of zooplankton exists on scales from the microscale (centimeters to meters) to the mesoscale (hun-

dreds of kilometers) (Mackas and Boyd 1979; Haury et al. 1978), patchiness itself can be viewed not as a sampling problem, but rather as a reflection of natural distributions. Avoidance and technical problems such as clogging and escapement (Vannucci 1968) represent sampling biases which tend to obscure our picture of these natural distributions. Although clogging and escapement are still important sources of error, improved net design can, in many instances, eliminate these as major problems (Smith et al. 1968). Zooplankton avoidance of nets, at least for some species, remains as an important sampling problem.

Avoidance is variable, depending upon such factors as time of day; light regime; size, shape, and color of the net; speed of tow; species; sex or developmental stage of the organisms; their physiological state; and absolute density (Fleminger and Clutter 1965; Isaacs 1965; McGowan and Fraundorf 1966; Brinton 1967; Clutter and Anraku 1968; Laval 1974; Boyd et al. 1978). Almost certainly this diversity of factors is one of the major reasons for a lack of consensus regarding the extent or magnitude of avoidance bias for

¹Contribution No. 4796 from the Woods Hole Oceanographic Institution, Woods Hole, Mass.

²Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

³Oceanic Biology Group, Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA 93106.

any particular zooplankton group. Further, the mechanisms by which an oncoming net is detected and avoided are not well known (Clutter and Anraku 1968).

Theoretical studies of avoidance (Barkley 1964, 1972; Clutter and Anraku 1968; Murphy and Clutter 1972; Laval 1974) have drawn attention to important behavioral aspects of avoidance and how these behavioral features are likely to interact with net size and towing speed. Avoidance theory provides a framework for the design of avoidance field studies and the interpretation of their results, as Barkley's (1972) examples clearly demonstrated. We have applied avoidance models to data on the euphausiid *Nematoscelis megalops* to determine its response to different net types under different conditions. Since our data on this relatively abundant species indicated substantial avoidance effects, we have examined it in some detail.

In studies of *N. megalops* vertical distributions (Wiebe and Boyd 1978; Boyd et al. 1978) night tows were consistently observed to produce higher numerical density estimates than tows at the same station during the day. These tows were taken with a multiple net system with a 1 m² mouth opening (MOCNESS, Wiebe et al. 1976). Although horizontal patchiness may have contributed in an unbiased way to the day/night differences in catch rate, the overall comparison of day and night tows strongly suggested greater avoidance during the day. Unfortunately, there were too few day/night pairs at a single station to demonstrate this by pairwise comparison.

During 1976 and 1977, as part of a multidisciplinary study of Gulf Stream cold core rings (Lai and Richardson 1977; Richardson 1980), more complete observations of day/night vertical distributions were made at stations in Slope Water and cold core rings. Tows were taken with a 1 m² MOCNESS and with a 10 m² MOCNESS. As will be demonstrated below, both net systems catch *N. megalops* without apparent size discrimination between the two. Both net systems are avoided to a certain extent, based on day/night catch ratios, but some revealing differences are evident. Using data from both sizes of nets, it is possible to apply Barkley's (1972) avoidance model to obtain independent estimates of the parameters of reaction distance and percent capture within a certain animal size range, and through a comparative analysis reach some tentative conclusions regarding avoidance mechanisms in the species studied.

METHODS

The combinations of 1 m² and 10 m² MOCNESS tows were taken at nine stations (Fig. 1), with additional information about each tow in Table 1. Stations 1-4 were sampled in April 1977 on RV *Knorr* cruise 65 and stations 5-9 were sampled on *Knorr* 71. Station 1 was in cold core ring "Bob," a 2-mo old ring; station 2 in ring "Al," a 6-mo old ring; station 6 in "Emerson," a relatively old ring; stations 7 and 8 in "Franklin," a middle-aged ring. The other stations were located in the Slope Water. For some comparisons data collected with the 1 m² MOCNESS on earlier cruises will be used; information about these tows (those noted in Table 2) is reported by Ortner et al. (1978). Station positions for the remaining tows are given in Table 1.

At the majority of stations day and night tows were taken with both the 1 m² and 10 m² MOCNESSes. The 1 m² net was equipped with nine nets of 333 μ m nylon mesh netting dyed dark blue and was fished obliquely so that eight strata were sampled. Generally, the strata sampled were 1,000-850, 850-700, 700-550, 550-400, 400-300, 300-200, 200-100, 100-0 m; usually between 600 and 1,000 m³ were filtered in each strata. Occasionally in the Slope Water when sharp hydrographic gradients were present, the sampling intervals were modified to bracket the physical discontinuities.

The 10 m² MOCNESS is a scaled up version of the 1 m² net system described by Wiebe et al. (1976). On the tows reported here, it was equipped with five nets of 3 mm nylon mesh white netting. This net system was fished obliquely with four of the five nets sampling 250 m intervals from 1,000 to the surface. Each net filtered between 13,000 and 43,000 m³. As with the 1 m² MOCNESS, the first net is fished while lowering the system to the maximum depth of the tow to provide uniform drag and to prevent kiting of the system at the start of the stratified oblique haul. Neither system has a bridle in front of the nets.

The nets of both systems are opened and closed with commands sent via conducting cable from a surface deck unit. For both systems on *Knorr* 65, we used an underwater unit which measures and telemeters to the surface depth temperature, conductivity, angle of the net system from the vertical, flow past the net, and information regarding the electrical and mechanical function of the opening/closing mechanism. The trans-

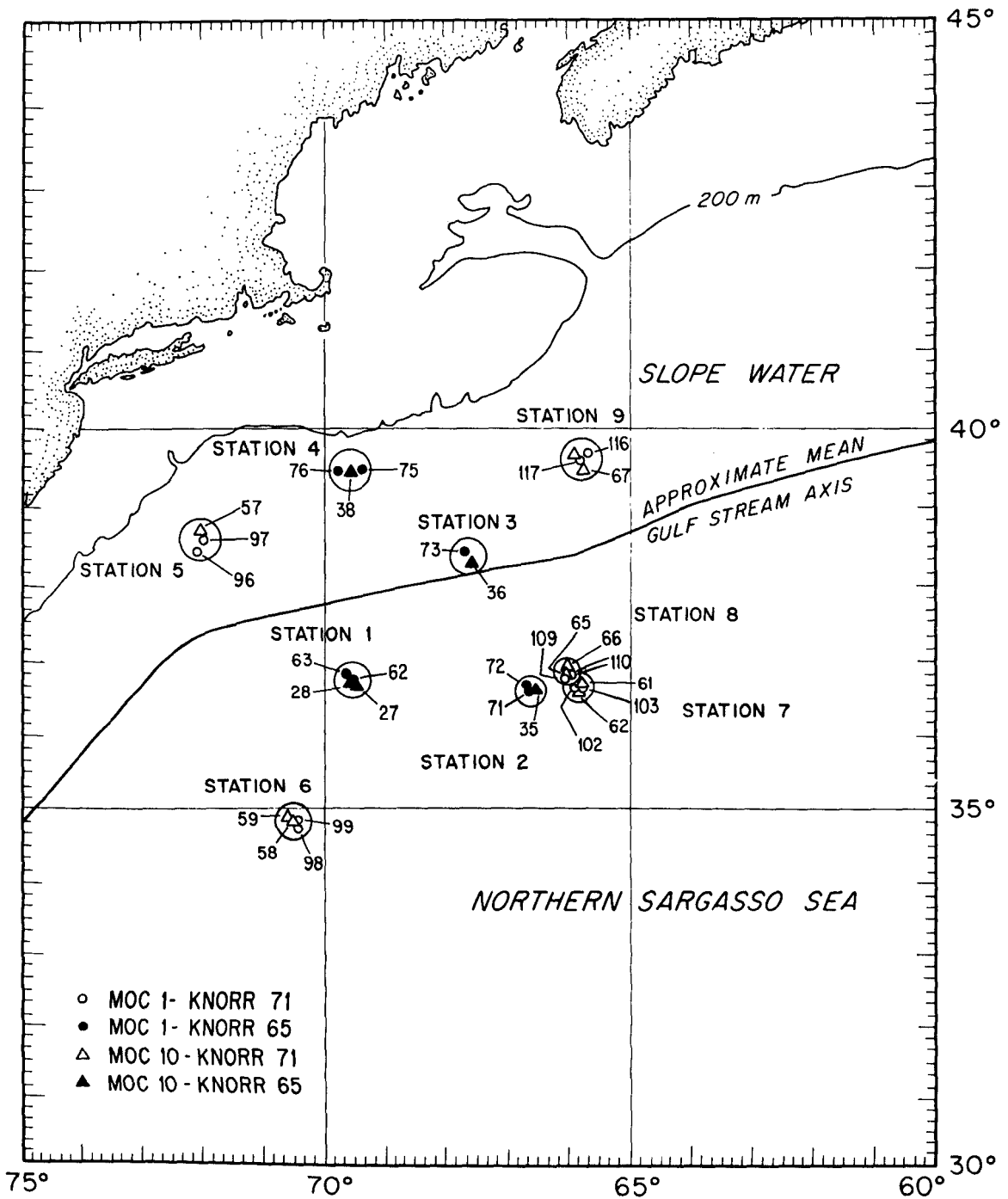


FIGURE 1.—Position of the 1 m² and 10 m² MOCNESS tows within each of the nine station areas (indicated by large open circles). Small solid triangles and circles are night tows; open ones are for day tows. Each tow listed in Table 1 is designated by its tow number.

TABLE 1.—Summary of tow statistical information for the 1 m² and 10 m² MOCNESS (MOC-1, MOC-10) tows taken in 1977 at the nine station locations illustrated in Figure 1. D = Day; N = Night.

Cruise no.	Station no.	MOC 1	Longitude W	Latitude N	Time of tow	MOC 10	Longitude W	Latitude N	Time of tow	Date of tow	MOC 1/MOC 10 10° isotherm depth (m)	
Knorr 65	1	62 D	69°30.1' 69°30.8'	36°43.2' 36°47.8'	1019- 1228	27 D	69°30.0' 69°25.9'	36°46.5' 36°38.6'	1352- 1744	4/17	300/330	
		63 N	69°33.0' 69°34.8'	36°49.0' 36°53.2'	0115- 0335	28 N	69°30.0' 69°27.2'	36°41.1' 36°49.0'	2055- 0030	4/17-18	296/270	
	2	72 D	66°39.0' 66°38.8'	36°38.0' 36°35.6'	0910- 1128	35 D	66°36.9' 66°34.4'	36°35.6' 36°31.3'	1303- 1650	4/24	717/690	
		71 N	66°39.6' 66°39.0'	36°30.5' 36°36.2'	2100- 2322					4/23		
	3	73 D	67°42.4' 67°37.5'	38°19.3' 38°21.3'	0955- 1128	36 D	67°37.0' 67°37.4'	38°21.3' 38°11.7'	1248- 1639	4/28	234/290	
		4	76 D	69°41.3' 69°38.0'	39°24.0' 39°28.0'	0705- 0913					4/30	
	75 N		69°26.6' 69°31.9'	39°28.5' 39°25.1'	2107- 2314	38 N	69°31.0' 69°43.0'	39°24.6' 39°21.1'	2345- 0345	4/29-30	200/255	
	Knorr 71	5	96 D	72°03.0' 72°00.0'	38°25.9' 38°29.9'	0930- 1204					10/23	
			97 N	71°54.5' 71°52.1'	38°36.8' 38°40.6'	2201- 0015	57 N	71°54.1' 71°51.0'	38°39.9' 38°47.0'	0052- 0050	10/23-24	190/190
		6	98 N	70°20.2' 70°21.5'	34°46.5' 34°50.2'	2150- 0005	58 N	70°21.9' 70°16.0'	34°50.8' 34°52.0'	0201- 0501	10/28-29	545/550
			7	102 D	65°52.1' 65°47.0'	36°40.1' 36°42.3'	0471- 1104	61 D	65°46.9' 65°40.0'	36°43.0' 36°46.0'	1345- 1652	11/3
		103 N		65°53.5' 65°47.9'	36°40.0' 36°42.5'	2243- 0059	62 N	65°48.9' 65°40.0'	36°42.2' 36°48.0'	0123- 0502	11/3-4	360/330
8		109 D	66°00.0' 66°00.8'	36°44.1' 36°49.1'	0910- 1138	65 D	65°58.3' 65°46.0'	36°49.0' 36°52.0'	1232- 1646	11/6	310/375	
		110 N	65°57.8' 65°59.5'	36°49.8' 36°55.1'	1901- 2123	66 N	65°58.8' 66°10.0'	36°56.0' 37°05.0'	2140- 0213	11/6-7	278-290	
9		117 D	65°51.1' 65°51.2'	39°32.9' 39°38.8'	1117- 1359	67 D	65°42.1' 65°48.0'	39°26.0' 39°33.0'	1308- 1628	11/15	200/230	
			116 N	65°47.0' 65°45.6'	39°35.0' 39°40.6'	1933- 2156	68 N	65°49.0' 65°51.0'	39°36.8' 39°35.0'	0026- 0500	11/15-16	232/205

mitted data were recorded on magnetic tape. They were also processed by a shipboard computer (Hewlett-Packard⁴ 2100) and plots of depth versus temperature and salinity were produced. On *Knorr 71*, the 10 m² net was deployed with a simplified electronics package which did not have a conductivity sensor and which transmitted data at a slower rate. For this latter system, plots of depth versus temperature and angle of the net were made with a Hewlett-Packard X, Y, Y recorder. During all of these tows, net speed, as indicated by the flowmeter, was closely monitored and adjustments to the ship speed and/or winch speed were made to keep the net moving ahead at 2±0.5 kn (3.71±93 km/h). All samples were preserved in 5-10% Formalin buffered to pH 8.0 with sodium borate.

For 162 of the 190 samples resulting from the tows listed in Table 1, we sorted and counted the entire sample for adult and adolescent (without

adult sexual characteristics) *N. megalops*. Very large catches were split with a Folsom plankton splitter (McEwen et al. 1954) and between one-half and one thirty-second of the sample was counted. Wet weights were determined either on all or a sizable fraction of the sorted individuals. Battered or disfigured individuals were excluded from this analysis. Individuals were blotted on absorbent paper and then weighed to ±0.1 mg on a Cahn model 7500 digital top-loader millibalance. Total body length (tip of rostrum to tip of telson) was determined on a small subset of individuals from both the *Knorr 65* and *71* collections in order to establish a relationship between wet weight and length (Fig. 2) for subsequent calculations of potential escape velocity based on body length. The geometric mean regression equation (Ricker 1973) which was fit to these data is similar to those presented by Mauchline (1967) for a variety of euphausiid species.

In some comparisons of the sampling capabilities of the two MOCNESSes and in the application of Barkley's (1972) avoidance theory, we have used the average numbers per 1,000 m³ for

⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—The ratio (Night/Day) of night 1 m² and 10 m² MOCNESS catch of *Nematoscelis megalops* (no./m²) divided by the paired day catch at stations in the Slope Water and cold core rings and the depth where the cumulated frequency of occurrence equals 50% in the night tow. Information about the tows taken on *Chain 125* and *Knorr 53* is given in Ortner et al. (1978).

Tow and cruise	Station or area	MOCNESS low no. (night/day)	Night/Day ¹	Depth of 50% (m)
1 m² MOCNESS				
<i>Knorr 65</i>	Station 1	63/62	5.6	82
	Station 2	71/72	33.0	80
<i>Knorr 71</i>	Station 4	75/76	1.5	340
	Station 5	97/96	5.9	345
<i>Chain 125</i>	Station 6	98/99	1.7	500
	Station 7	103/102	29.0	370
	Station 8	110/109	1.3	325
	Station 9	116/117	33.0	150
	Slope Water	120/21	63.4	220
<i>Knorr 53</i>	Slope Water	119/18	10.9	260
	Ring "D"	5/8	(²)	300
	Slope Water	35/37	48.9	280
	Slope Water	41/42	.57	380
	Slope Water	39/40	(²)	450
<i>Knorr 62</i>	Ring "D"	129/27	2.7	650
	Ring "D"	133/31	6.4	450
	Slope Water	57/58	1.5	245
<i>Knorr 62</i>	Ring "AI"	45/47	2.6	505
	10 m² MOCNESS			
<i>Knorr 65</i>	Station 1	28/27	3.67	130
<i>Knorr 71</i>	Station 6	58/59	2.66	700
	Station 7	62/61	0.68 (1.47)	375
	Station 8	66/65	0.84 (1.19)	370
	Station 9	68/67	2.93	180

¹Vertical distribution of *N. megalops* on these tows illustrated in figure 5 of Wiebe and Boyd (1978).

²None present in day collection.

the water column. These values were obtained by combining the stratified oblique hauls to form a composite tow. Note that because the water column sampled is 1,000 m, the integrated number per 1,000 m³ for the column is identical to numbers per square meter.

RESULTS

Analysis of 1 m² and 10 m² MOCNESS Observations

The vertical distribution of *N. megalops* at stations where pairs of 1 m² and 10 m² MOCNESS tows were taken (Fig. 3) illustrates the large variations in depth distribution that can occur in the different hydrographic regimes and at different times of year. As previously described by Wiebe and Boyd (1978), this species generally has its center of distribution above 300 m in Slope Water. Exceptions in Slope Water are associated with the presence of warm core rings. In young cold core rings such as "Bob," the center of distribution is also shallow. In most of the older rings we have sampled, the distribution of *N. megalops*

deepens as is evident in "Franklin" and "Emerson" (see also figure 5 in Wiebe and Boyd 1978).

Very close agreement between the two net systems in the shape of the vertical distribution is found, especially at night (Fig. 3). The night 1 m² and 10 m² MOCNESS tows also show significant agreement in the integrated numbers caught per square meter ($r = 0.99$; $P < 0.05$). In contrast, the paired day tow data are considerably more variable and do not show significant agreement in integrated numbers per square meter ($r = 0.13$; $P > 0.05$).

Clear evidence for differential day/night net avoidance by *N. megalops* is found in the catch data obtained by the 1 m² MOCNESS (Fig. 3). Without exception, for each of the eight day/night pairs of tows taken on *Knorr 65* and *Knorr 71*, the day estimate of numbers per square

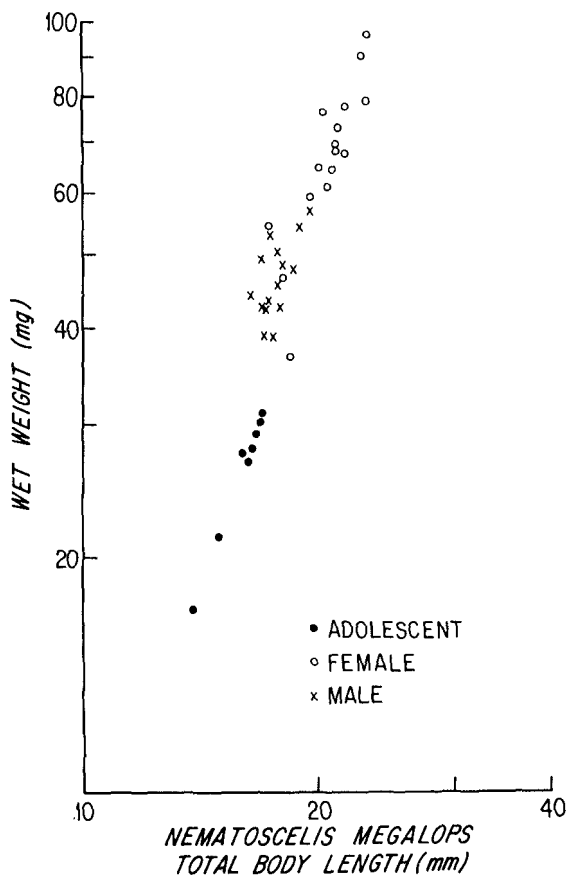


FIGURE 2.—Relationship between total body length, carapace length, and wet weight of *Nematoscelis megalops*.

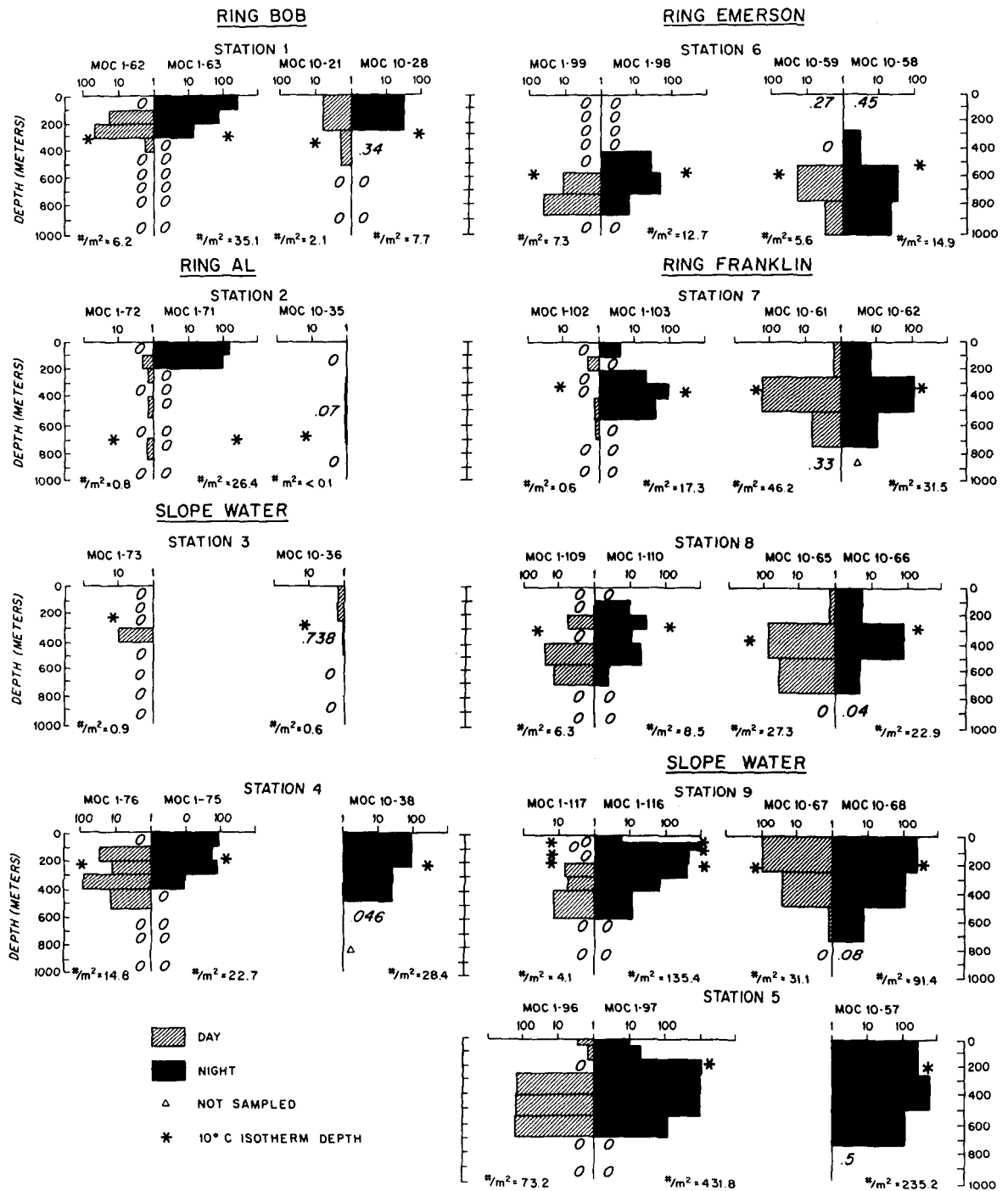


FIGURE 3.—Vertical distribution of *Nematoscelis megalops* in the Slope Water and in variously aged cold core rings based on collections made with the 1 m² and 10 m² MOCNESSes on two cruises taken 6 mo apart. Night samples are blacked; day samples are crosshatched.

meter for the water column is less than the corresponding night catch. In every case, sampling extended below the maximum depth of occurrence of the population and there is no evidence that any individuals of the population migrated vertically out of the depth zone sampled during the day. Therefore, it is highly significant that all of the day values were less than the respective night ones ($P < 0.005$). This result gains importance if we also consider 10 other day/night pairs of 1 m² MOCNESS tows in which *N. megalops* was collected on previous cruises (*Chain 125*, *Knorr 53*, *Knorr 62*). For nine of these pairs, moderately to dramatically higher catches in the night tow were obtained (Table 2). The single exception to this pattern was a pair of Slope Water tows taken near the continental shelf in the wake region of a warm core ring (tows 41, 42). But these two tows were displaced in space by several miles, and the night tow was taken nearer the warm core ring where a lower catch might have been expected.

Of the 18 day/night pairs of 1 m² MOCNESS tows, 17 yield higher density estimates at night. Patchiness in the distribution of *N. megalops* contributed to variability to these estimates but as an unbiased variance component, it does not affect our expectation that one-half of the day and one-half of the night tows in day/night pairs should be the larger. Thus it is unlikely that patchiness of this species is responsible for the significantly higher night catches that we have observed ($P < 0.001$). We know of no other explanation than avoidance to explain this result.

There are only five pairs of 10 m² MOCNESS observations of the vertical distribution of *N. megalops*. For two of these, the integrated day catch is larger than the corresponding night catch and, therefore, night catches are not significantly larger than day catches ($P > 0.05$). This result either means that there is no day/night differential avoidance of the 10 m² net or that in the face of other sources of error such as patchiness, we have too few day/night pairs of observations to observe the avoidance effect. If avoidance were affecting only the smaller net then at least we would expect that the 1 m² net day catches per unit volume would be consistently smaller than the corresponding 10 m² net day catches. We might also expect that night catches with the 1 m² net would be smaller than the 10 m² net. Neither comparison yields a significant result ($P > 0.05$; day MOCNESS 1 tows greater than

day MOCNESS 10 tows in four out of seven comparisons; night MOCNESS 1 tows greater than night MOCNESS 10 tows in three out of seven comparisons). Thus within the limits of error, by day or by night both net systems provide comparable estimates of the number of *N. megalops* living in the water column at a given station.

It is possible that the lack of differences in the catching rates between the two nets is due to the different mesh sizes. Small individuals might have been caught more efficiently by the 1 m² net while larger individuals could have avoided this net better and conversely for the 10 m² net except that small individuals would have been lost due to escapement through the mesh. The size-frequency data in Figures 4 and 5 do not support this possibility. While there is considerable variability between net tow pairs, in terms of absolute abundance, neither net system systematically catches large or small individual *N. megalops* in the size range counted better than the other. A similar observation can be made if comparisons are made on the relative abundances in a given size class (Fig. 6).

There is one other potentially significant trend in the data that is important to note. The magnitude of the day/night avoidance does not appear to be uniform with depth. For the 1 m² MOCNESS, largest differences between paired night and day catches where both are positive occur when the center of distribution of *N. megalops* is above 300-400 m and minimum differences occur at or below these depths (Table 2). Linear regression of the ratio of night to day catch (N/D) versus depth of the center of the distribution at night (50% of occurrence with depth) is significant at $P = 0.1$. There is a similar pattern in the 10 m² MOCNESS tows, although as mentioned above, the day/night differences in catching rates are considerably smaller.

In summary, there is clear evidence for differential day/night avoidance of the 1 m² MOCNESS. Furthermore, there are no significant differences in the size range of adolescent or adult *N. megalops* caught by the 1 m² or 10 m² MOCNESS systems nor in either system's estimates of its abundance in the water column at a given station when day or night pairs are compared. Although differences between pairs of day/night catches for the 10 m² MOCNESS are statistically not significant, the entire data set when considered as a whole strongly suggests that *N. megalops* is also avoiding the 10 m² net, albeit to a lesser extent.

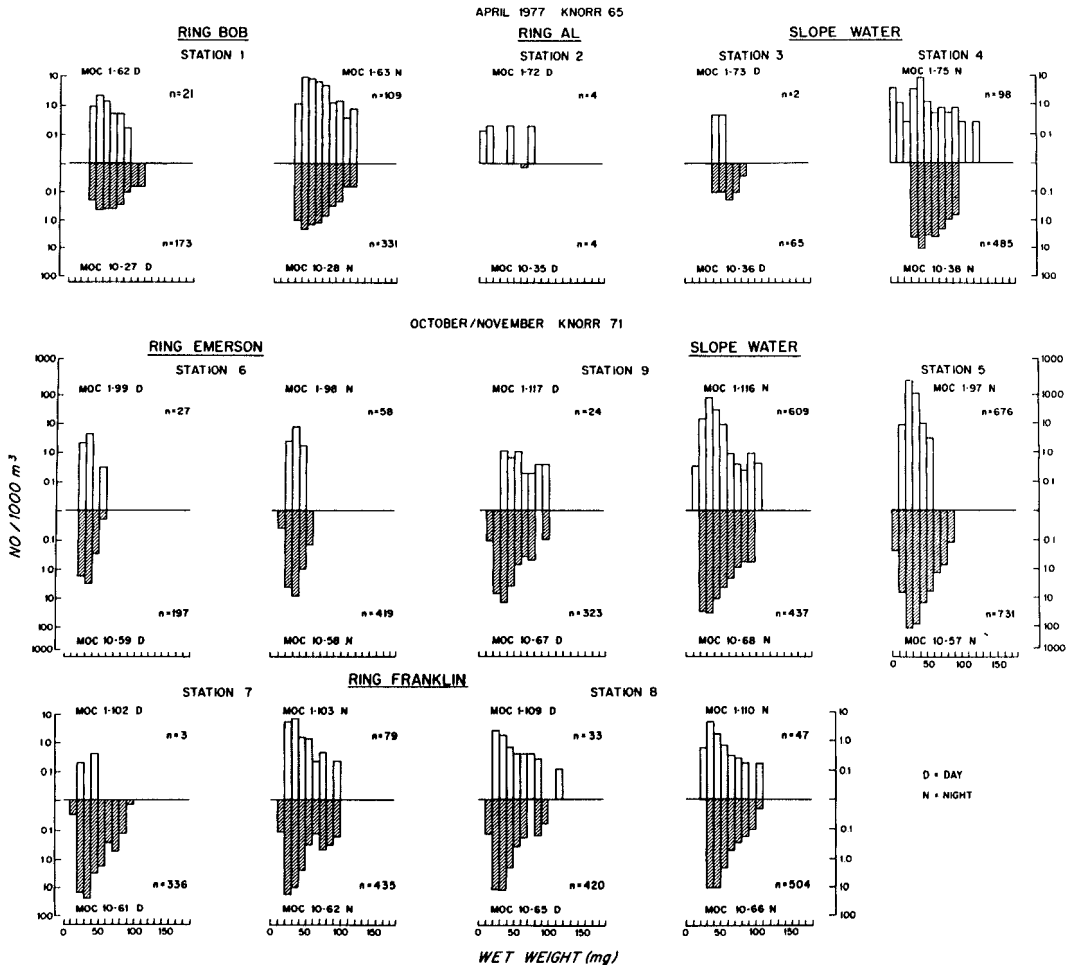


FIGURE 4.—Comparison of the composite size-frequency distribution (expressed as No./1,000 m³ for a given wet weight interval) of *Nematoscelis megalops* caught by the MOCNESS 1 (shaded) and the MOCNESS 10 (crosshatched) for tows taken on the same day or night. n = the number of individuals used to construct the histogram.

Application of Barkley Avoidance Theory

Since it is likely that *N. megalops* avoids both net systems, it must detect the approach of either net at some distance in front of the net, resulting in a response which permits a certain percentage of the population to avoid capture. Determination of the avoidance percentage and reaction distance requires an indirect approach, since no other means are available. The theoretical framework on the process of net avoidance developed by Barkley (1964, 1972) provides a means for estimating these parameters according to a quantitative theoretical model. Barkley (1972) formulated the problem in the following way:

$$\text{Catch} = (\text{volume sampled}) \times (\text{no. of organisms unit volume}) \times (\text{probability of capture}) - (\text{losses}) \quad (1)$$

“Losses” refers to individuals which are enclosed by the net but escape through the net meshes. For the size range of individuals which constitute our “catch,” the “losses” term is essentially zero. Since the volume of water sampled has been rather carefully measured, the “probability of capture” (P_c) is of greatest concern. P_c is related to the mean reaction distance (x_0), the radius of the net mouth (R), the net’s speed (U), and the organism’s mean escape speed (u_e) by the equa-

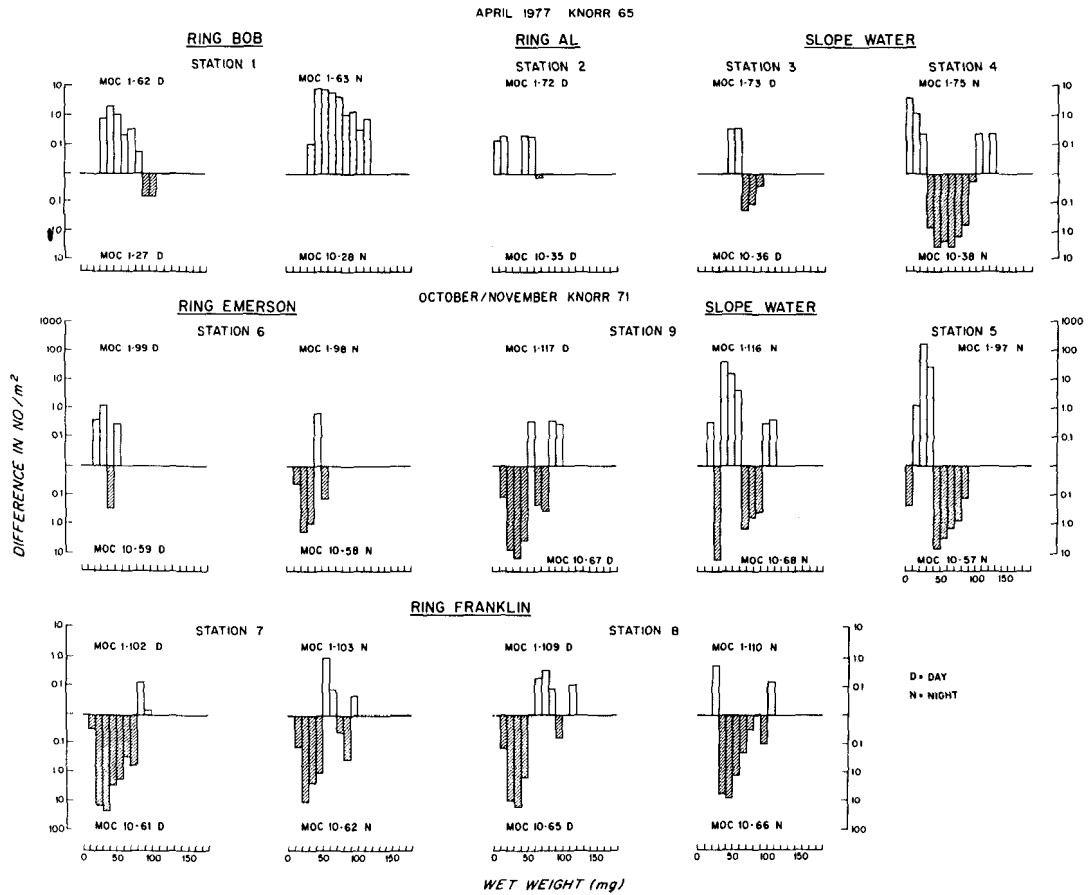


FIGURE 5.—Comparison of the difference between paired MOCNESS 1 and MOCNESS 10 catches in No./1,000 m³ for a given wet weight interval. For shaded columns above the line, the MOCNESS 1 catch is greater than the MOCNESS 10 catch and vice versa for crosshatched columns below the line.

tion derived by Barkley (1972, equation 6) wherein:

$$P_c = \left(1 - \frac{x_0 u_c}{R(U^2 - u_c^2)^{1/2}} \right)^2 \quad (2)$$

This expression assumes that as the net moves forward through the water, an individual senses the oncoming net and at a distance x_0 in front of the net begins a swimming response in a direction away from the net which is optimal for avoidance. Thus, this equation provides an estimate of the minimum probability of capture.

As a first step in applying these equations to our data, we may recall that for both the paired night tows and the paired day tows differences between the two net systems were not significant, i.e.,

$$\frac{10 \text{ m}^2 \text{ MOCNESS catch}}{\text{volume sampled}} \cong \frac{1 \text{ m}^2 \text{ MOCNESS catch}}{\text{volume sampled}}$$

If we assume that the number of organisms per unit volume was a constant during the time each pair of tows was taken, then:

$$10 \text{ m}^2 \text{ MOCNESS } P_c = 1 \text{ m}^2 \text{ MOCNESS } P_c$$

and

$$\left(1 - \frac{x_{10} u_c}{150(100^2 - u_c^2)^{1/2}} \right)^2 = \left(1 - \frac{x_1 u_c}{50(100^2 - u_c^2)^{1/2}} \right)^2$$

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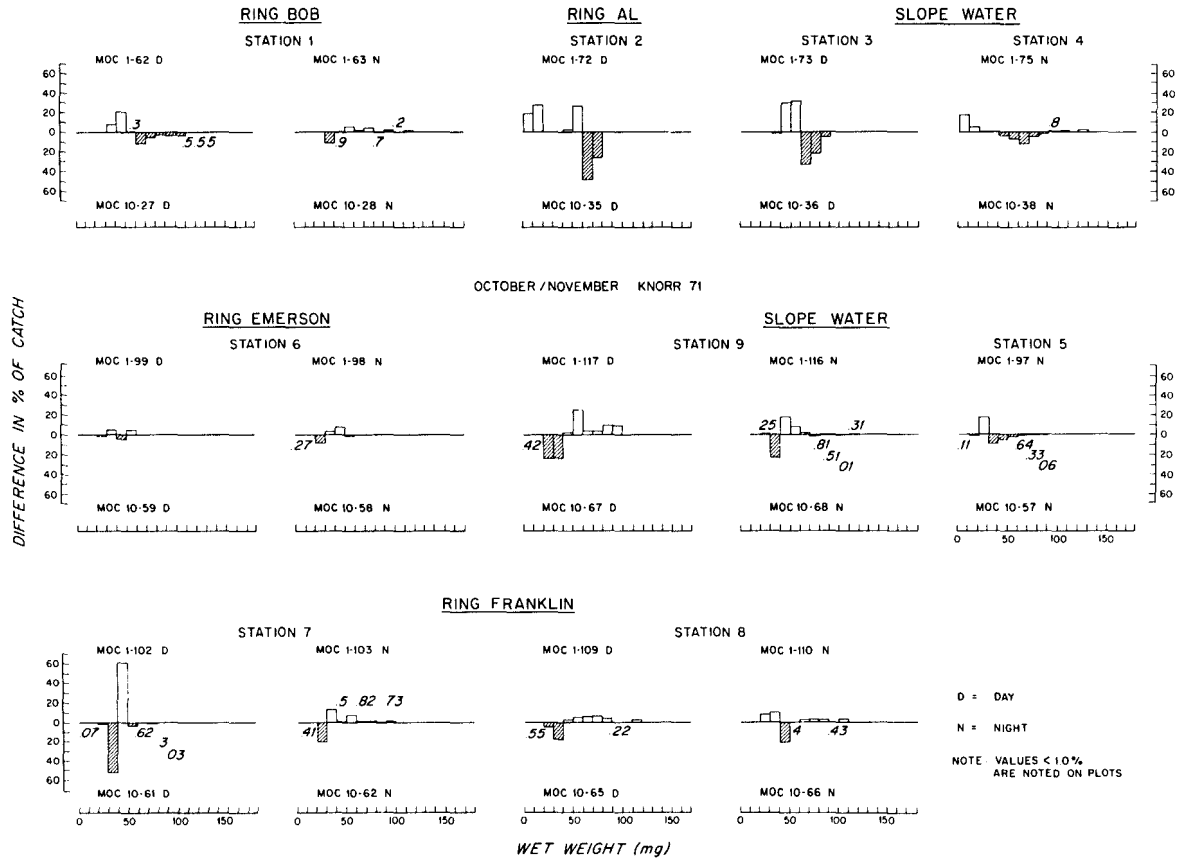


FIGURE 6.—Comparison of the difference between paired MOCNESS 1 and MOCNESS 10 tows in the percent of the catch in a given wet weight interval.

where x_{10} and x_1 refer to the reaction distance for the 10 m² and 1 m² net systems, where we have approximated the radius of the large net as 150 cm and the small net as 50 cm, and where both nets were towed at approximately 100 cm/s. We are also assuming that the mean swimming speed of the individuals (u_e) is the same for both nets. Solving for the ratio of the reaction distances we find:

$$\frac{x_{10}}{x_1} = 3.0.$$

That is, in order for the two net systems to provide numbers of *N. megalops* per volume filtered which are approximately the same, the reaction distance for the 10 m² MOCNESS must be three times greater than for the 1 m² MOCNESS.

Since we do not know the absolute abundance of *N. megalops* independent of our net tow estimates for any sampling period, we cannot directly estimate the absolute magnitude of the reaction distance or the minimum probability of capture for either net. It is possible to derive those estimates by a method described by Barkley (1972:808) which involves making a best fit of theoretically derived curves which relate P_e , u_e/U , and X_0/R to observations of u_e/U and the catch/volume filtered for each size class of individuals caught by the nets. In order to make these comparisons, we must have an estimate of the mean escape velocity of an individual (u_e) in a given size class, and ultimately we must make some assumption about population structure, i.e., abundance versus size class of the population sampled.

To make estimates of u_e , we have followed Barkley (1972) and used generalized swimming speed-body length relationships because there is no direct information about u_e for *N. megalops*. However, as discussed below, inconsistencies between model expectations and the field data develop when this assumption is applied. Our basic size-frequency data are in units of wet weight. However, as noted under "Methods," a subset of individuals of *N. megalops* from MOCNESS 10 tows were used to establish the relationship between wet weight and body length (Fig. 2). Mean body wet weight of individuals in each size class was converted to body length (L) and then to relative escape speeds (u_e/U) assuming initially that $u_e = 10 L$. This assumption is supported by work of Kils (1979) and Semenov (1969). Relative escape speeds were plotted versus the catch/1,000 m^3 in each size class on semilog graph paper

scaled so that each plot could overlay a reproduction of the upper panel of Barkley's figure 3 (1972:805). These plots were adjusted vertically to obtain a "best" fit with the x_0/R curves such that a maximum number of points fell between any two of the x_0/R curves (Fig. 7). This produces an estimate of x_0 if it is assumed that the shape of the size-frequency distribution is entirely produced by improvement of avoidance capability with increasing size.

Estimates of reaction distance (x_0) for each net system (Table 3) are between 1.7 and 2.3 for the 1 m^2 MOCNESS and between 4.9 and 6.6 m for the 10 m^2 MOCNESS. No significant differences between night x_0 's and day x_0 's for either net system are observable. Our initial conclusion was that this was an unreasonable result since intuitively one would expect an increased night catch to be related to reduced nighttime x_0 values

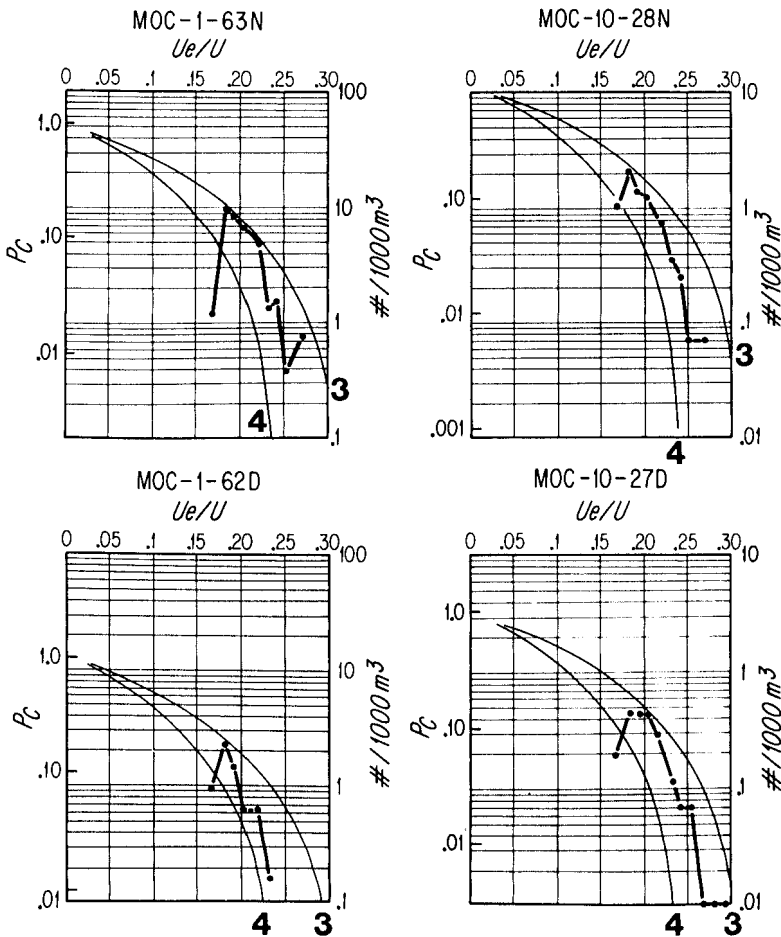


FIGURE 7.—Examples of relative escape speed of *Nematoscelis megalops* individuals versus the catch per 1,000 m^3 . Superimposed on this plot are the theoretically derived curves of x_0/R as a function P_c and u_e/U adjusted to give a "best" fit of the observed points.

if individual escape speeds remained constant. However, further analysis reveals that the difference in x_0 for a given day/night catch differential could be a function of the relationship between the observed night catch and the true water column abundance. This is clearly evident if we express the ratio of the day catch per vol-

It could be argued that the day/night catch differential is due to differences in escape speed of the individuals rather than a change in their reaction distance. To explore this we have also solved Equation (3) for the ratio of day escape speed, u_D , to night escape speed, u_N , after assuming $x_D = x_N$.

$$u_D/u_N = \frac{\left[\left(\frac{DC}{A} \right)^{\frac{1}{2}} - 1 \right]^2 * \left[\left(\frac{NC}{A} \right)^{\frac{1}{2}} - 1 \right]^2 + \left[\left(\frac{DC}{A} \right)^{\frac{1}{2}} - 1 \right]^2 * \left[\frac{X_n}{R} \right]^2}{\left[\left(\frac{DC}{A} \right)^{\frac{1}{2}} - 1 \right]^2 * \left[\left(\frac{NC}{A} \right)^{\frac{1}{2}} - 1 \right]^2 + \left[\left(\frac{NC}{A} \right)^{\frac{1}{2}} - 1 \right]^2 * \left[\frac{X_n}{R} \right]^2} \quad (5)$$

ume sampled (DC) and night catch per volume sampled (NC) in terms of real abundance (A) and percent capture as expressed in Equation (2):

Note that the ratio of day/night escape speeds is a function of x_N and R as well as DC , NC , and A . The escape speed and radius of net were not in

$$\frac{DC}{NC} = A \left(1 - \frac{x_D}{R \sqrt{\frac{U^2}{u_D^2} - 1}} \right)^2 / A \left(1 - \frac{x_N}{R \sqrt{\frac{U^2}{u_N^2} - 1}} \right)^2 \quad (3)$$

If we assume that the daytime escape speed, u_D , is equal to the nighttime speed, u_N , and solve for the ratio of the daytime reaction distance, x_D , to the nighttime reaction distance, x_N , we have:

Equation (4) for the ratio of day/night reaction distances. We have evaluated this ratio using the same values noted above. With these results (Fig. 8b), we reach a conclusion similar to that for re-

$$x_D/x_N = \left(\frac{DC}{NC} \right)^{\frac{1}{2}} + \frac{1}{1 - \left(\frac{NC}{A} \right)^{\frac{1}{2}}} - \frac{\left(\frac{DC}{NC} \right)^{\frac{1}{2}}}{1 - \left(\frac{NC}{A} \right)^{\frac{1}{2}}} \quad (4)$$

We have evaluated this equation assuming a true abundance of 100 individuals per volume, nighttime catches of 99, 90, 10, 1, and 0.1 individuals per volume, and daytime catches of 50, 10 and 1% of the nighttime catch. The ratios of x_D/x_N , plotted as a function of the ratio of NC/A Fig. 8a), shows that only very small differences in reaction distance between day and night are required to explain large day/night catch differentials when the night catch is 10% or less of the true water column abundance. The fact that we see no significant difference in day/night reaction distances suggests our nighttime catches also could be affected strongly by avoidance, and that even at night we have significantly underestimated the numbers of *N. megalops* in the water column.

action distance, namely, if reaction distance remains constant between day and night, then small differences in escape speed can explain the day/night catch differential when the night catch is 10% or less of the true abundance.

There is, however, an entirely different explanation which may account for this outcome in application of Barkley avoidance theory to our data. In fitting these data to Barkley's plots of percent capture versus the ratio of x_0/R , two assumptions were required: 1) that all changes in size frequency are due to avoidance and 2) that swimming speed is a function of body size. The second assumption can be examined if one has day/night pairs of tows taken at the same station location with the same size of net. With swimming speed a function of size, Barkley's model

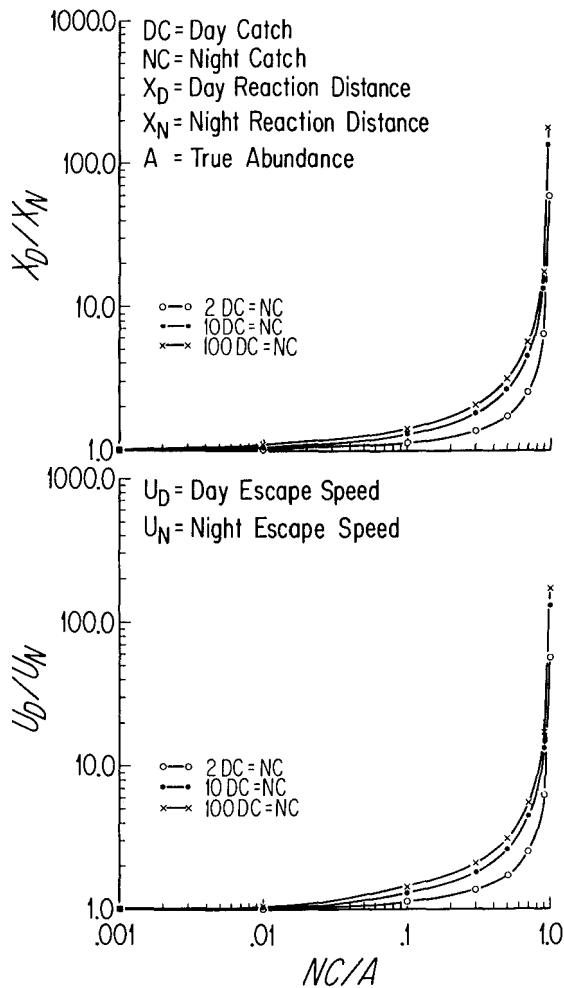


FIGURE 8.—Relationships between the ratio of night catch to true abundance (NC/A) and a) the ratio of day and night reaction distances (x_D/x_N), and b) the ratio of day and night escape speeds (u_D/u_N).

predicts that the ratio of the number of individuals caught per size class at night (NC) to those caught during the day (DC) will increase with increasing individual size (the inverse of Equation 3).

This relationship is illustrated in Table 4 where u_N and u_D are assumed to be equal and 10 body lengths/s, $x_D = 175$ cm, $x_N = 150$ cm, $R = 50$ cm, and $U = 100$ cm/s. This ratio increases dramatically with individual size until at the largest size, the model predicts all individuals avoid capture. No such pattern emerges if we compute the ratio NC/DC for each size class in our paired day/

TABLE 3.—*Nematoscelis megalops* reaction distances (x_0) for the 1 m² and 10 m² MOCNESS nets derived from the plots like those in Figure 7.

Station	Cruise	Tow	Day/Night	x_0/R	x_0
1	Knorr 65	M-1-62	D	3.4	1.7
		M-10-27		3.3	5.0
		M-1-63	N	3.4	1.7
		M-10-28		3.4	5.0
3	Knorr 65	M-1-73	D	3.4	1.7
		M-10-36		(¹)	(¹)
4	Knorr 65	M-1-75	N	(¹)	(¹)
		M-10-38		3.4	5.0
5	Knorr 71	M-1-97	N	4.5	2.3
		M-10-57		4.4	6.6
6	Knorr 71	M-1-99	D	4.5	2.3
		M-10-59		4.4	6.5
		M-1-98	N	4.5	2.3
7	Knorr 71	M-10-58		4.4	6.6
		M-1-102	D	4.4	2.2
		M-10-61		(¹)	(¹)
8	Knorr 71	M-1-103	N	4.4	2.2
		M-10-62		4.4	6.6
		M-1-109	D	3.5	1.8
9	Knorr 71	M-10-65		4.4	6.6
		M-1-110	N	4.3	2.2
		M-10-66		4.3	6.4
9	Knorr 71	M-1-117	D	3.5	1.8
		M-10-67		4.4	6.6
		M-1-116	N	4.4	2.2
		M-10-68		4.3	6.5

¹Not sufficient points to derive an estimate; Station 2 omitted for this reason.

TABLE 4.—The ratio of night catch to day catch as a function of individual swimming speed (u_0) as predicted by Barkley's avoidance model (inverse of Equation 3). u_0 is assumed to be a function of body size as described in the text.

Body wet weight (mg)	u_0 (cm/s)	Night catch ¹	Day catch ¹	Ratio
20	15.08	0.294	0.217	1.35
30	16.32	0.253	0.177	1.43
40	17.56	0.216	0.141	1.53
50	18.80	0.181	0.108	1.66
60	20.04	0.149	0.080	1.84
70	21.28	0.120	0.056	2.12
80	22.52	0.093	0.036	2.57
90	23.76	0.070	0.020	3.42
100	25.00	0.050	0.009	5.47
110	26.24	0.033	0.002	14.57
120	27.48	0.022	0.000	—

¹Catch units are proportion of individuals present per unit volume.

night MOCNESS 1 or MOCNESS 10 tows (Table 5). Thus, the assumption of increasing swimming speed with increasing size does not appear to be valid, i.e., for the size range of individuals used in this study, avoidance swimming speeds are essentially the same. One implication of this finding is that the size-frequency distributions evident in the field data may not be seriously biased by the avoidance although the estimates of average density clearly are.

TABLE 5.—Ratios of night to day catches (number per square meter) of *Nematoscelis megalops* as a function of size for stations where both the MOCNESS 1 and the MOCNESS 10 were taken. ∞ indicates only the night tow caught individuals in the given size class; 0 indicates the opposite patterns.

Body wet weight (mg)	MOCNESS 1—tow no.:					MOCNESS 10—tow no.:				
	117/116	62/63	99/98	102/103	109/110	27/28	59/58	61/62	65/66	67/68
10	∞	—	—	—	—	—	∞	4.4	0	0
20	∞	—	1.2	33.3	0.3	—	2.4	1.1	<0.1	4.0
30	66.6	1.3	1.7	∞	2.6	5.9	2.6	0.4	0.8	2.2
40	45.5	4.0	∞	3.7	2.6	4.8	3.6	0.8	4.8	2.9
50	7.9	5.6	0	∞	1.9	3.6	7.7	0.2	5.6	5.9
60	4.6	1.1	—	∞	0.8	3.2	—	0.5	2.8	5.9
70	2.1	7.7	—	∞	0.7	2.6	—	0.9	∞	1.8
80	0.6	7.7	—	—	0.7	2.9	—	2.5	1.0	∞
90	2.4	∞	—	—	∞	3.5	—	12.5	1.7	6.3
100	∞	∞	—	—	∞	1.0	—	—	∞	—
110	—	∞	—	—	0	7.1	—	—	—	—
120	—	—	—	—	—	0	—	—	—	—
130	—	—	—	—	—	0	—	—	—	—

DISCUSSION

From this application of the Barkley avoidance theory, it appears that estimates of *N. megalops* water column abundance could be substantially underestimated by both nets, even at night. Minimum probabilities of capture derived from best fits to model expectations are 0.1 or less for night catches and 0.01 or less for day catches. However, the fact that we cannot demonstrate a dependence of the ratio of night to day catches on the size of individuals caught strongly suggests the size dependent swimming speed assumption required to apply the model is not valid for this species, a result which is apparently supported by Kils's (1979) data for *Euphausia superba* escape swimming (tail swimming). Being unable to make this assumption means that the field population size-frequency distribution which was observed is probably not materially affected by avoidance. Undeniably some fraction of the *N. megalops* population is avoiding the net systems, and the problem is serious enough to merit an effort to reduce this bias, i.e., to prevent the avoidance from taking place.

The usual strategies suggested to reduce net avoidance, increasing net speed or net size, have serious shortcomings in this case. Our evidence strongly implies that *N. megalops*' response to increased net size is to increase its reaction distance so that the catch rate remains relatively constant. Barkley (1972) reached the same conclusion in a comparison of 1 m diameter net and 3 m IKMT (Isaacs-Kidd midwater trawl) catching rates of the northern anchovy, *Engraulis mordax*. It is possible that by going to still larger nets (i.e., >10 m² mouth areas), a reduction in the bias could be effected. However, larger nets would be

impractical, if not impossible, to handle on most oceanographic vessels.

As Barkley (1964) has demonstrated, increased net speed is not a feasible strategy for avoidance reduction since increasing the towing speed of a net requires a compensatory reduction in net size. The practical limits to increasing the tow speed are reached at 2 to 3 kn, because of unavoidably extreme wire angles and inordinate amounts of wire required to fish even at moderate depths (to 1,000 m). High speed tows generally result in damaged specimens, reducing their value in studies requiring taxonomic identification or in physiological and biochemical measurements. Finally, as speed of net is increased, the effects of escapement through the meshes is enhanced.

Another means of reducing avoidance, that of camouflaging the net to reduce an animal's ability to detect its presence and thereby reducing the avoidance reaction distance, has been discussed briefly by Clutter and Anraku (1968). There is evidence that it may be an effective strategy for species such as *N. megalops* (LeBrasseur and McAllister, unpublished data cited by Clutter and Anraku 1968). To use this approach, one must first know what kind of a signal the animal is using to detect the oncoming net. Camouflaging the net can be accomplished by reducing the signal until it becomes part of the background (omnidirectional noise). Alternatively, the noise level could be increased until the signal is no longer detectable.

Signals emanating from a net and towing cable include deformation of flow, near field (displacement dominant) or far field (pressure dominant) sound, and light (bioluminescence) (Clutter and Anraku 1968). The importance of

these different signals obviously depends upon the net structure and towing cable configuration and upon the ability of *N. megalops* to sense the various signals. Although there is no direct experimental information about *N. megalops*' sensory capabilities or about the signals being generated by MOCNESS, it seems clear that the primary avoidance stimulus involves day to night variations in light. *Nematoscelis megalops* must use vision to detect the net and can better avoid the net during the day than at night because during the day the net is better illuminated. A fundamental link between the amount of light present and the magnitude of the avoidance is provided by our observation that as individuals live deeper in the water column under substantially reduced daytime light levels, day/night differences in catch rates decline.

But if we accept the results gained by the application of Barkley's model which indicate substantial avoidance takes place at night in the absence of bright sunlight, then other factors must also be important. We propose that bioluminescence is the principal signal and that vision remains the principal means of detection.

Three lines of evidence support the importance of bioluminescence as an avoidance cue. First, in an experiment conducted in the early 1960's, Boden (1969) equipped an IKMT with light meters so that he could monitor the amount of light produced above, below, in front of, and inside the trawl as it was towed at night. Bioluminescent light above the trawl was less than below the trawl but both were considerably lower than that ahead of or in the net. Light within the net was so bright that it recorded off scale and individual flashes were often too numerous to be recorded as such. Light ahead of the net was also exceedingly bright. Boden (1969) speculated that the light ahead of the net was caused by organisms flashing either in response to the light within the net or to pressure or sound waves propagating forward from the net. Second, Neshyba's (1967) experiments with a submarine photometer and strobe light showed that mesopelagic and epipelagic organisms could be stimulated to produce significant amounts of bioluminescence (10^{-4} $\mu\text{W}/\text{cm}^2$) for a sustained period by proper strobe light flashing. In the absence of artificial flashing, he observed a much lower level of irregular flashing (10^{-8} - 10^{-7} $\mu\text{W}/\text{cm}^2$) similar to that reported by Kampa and Boden (1956), Clarke and Backus (1964), and Boden et al. (1965). Third, it is known that the

eyes of euphausiids and decapod shrimps living at midwater depths during the day (i.e., 200-600 m) are sensitive to light levels (10^{-7} to possibly 10^{-9} $\mu\text{W}/\text{cm}^2$, Clarke 1970) significantly lower than that produced as a result of bioluminescence.

These lines of evidence suggest that the light generated by organisms when they come in direct contact with the nets or encounter turbulence caused by the net is used by individuals ahead of the net to detect its presence and begin an avoidance response. It seems likely that the light ahead of the net observed by Boden (1969) was caused by the same kind of response mechanism described by Neshyba (1967), i.e., flashing in response to flashing.

The tactic of reducing the visual contrast between a net and the surrounding water was demonstrated by LeBrasseur and McAllister (unpublished data cited by Clutter and Anraku 1968) to reduce the avoidance error for euphausiids both day and night. However, if bioluminescence in and ahead of the net is an important cue as we suspect it to be, then a more active means of camouflaging the net is required.

It is known from recent evidence (Warner et al. 1979) that decapod crustacea living at the same depth as *N. megalops* are easily "blinded" by even moderate amounts of light. This suggests the possibility of equipping the mouth of a net with a "blinding" light system to be used to periodically illuminate a region ahead of the net with enough light to temporarily blind individuals in the net. With the light out, individuals so affected by the light pulse would be unable to see and, therefore, to respond to the much lower light generated by zooplankton being captured by the net. We postulate that individuals outside the zone of temporary blindness may respond by electing a startle response, but, because the volume illuminated would be so large, their movement would be random with respect to the volume to be filtered by the net. Clearly, considerably more research is required before this strategy could be considered feasible.

There are two precautionary notes that must be made. First, in spite of avoidance error, vertical distribution patterns obtained in sampling this species with MOCNESS at different times under different hydrographic regimes are replicable (Fig. 3). That is, although avoidance error is strongly affecting the numerical estimates, the shape of the vertical distributions seem much less affected. Thus, in spite of the avoidance, we believe we are obtaining valuable ecological in-

formation about this species. Second, for most species of euphausiids and many copepods, chaetognaths, and pteropods in our collections, we have no evidence that differential day/night avoidance is taking place. Therefore, for many ecological studies of oceanic zooplankton, nets still seem the most effective tool to use to quantitatively collect them.

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