A COMPARISON OF EUPHAUSIID ABUNDANCES FROM BONGO AND 1-M CalCOFI NETS

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ABSTRACT

Abundances of 12 species of euphausiids were determined from net tows designed to compare catching capacities of a 1-m ring net having an anterior towing bridle and a bridleless Bongo sampler having nets of either 60- or 71-cm mouth width. Replicate tows consisted of the 1-m and the Bongo towed consecutively, obliquely to 210-m depth. Because many euphausiids migrate to considerable depths for the daytime, only nighttime samples were used in determining relative efficiencies of the nets.

For each species, determinations were made of differences between average abundances from Bongo and 1-m net samples. Abundances were compared at each 1-mm increment of body length. Larvae were more abundant when determined from samples from the 1-m net. Juveniles and adults were better retained by the Bongo. Total numbers differed little for most species.

After the larval phase, the ratio of Bongo catch to 1-m-net catch usually increased with body length until near maximum size. This led to significantly greater estimates of biomass from the Bongo samples. In the two species for which males and females were analysed separately, proportions of the sexes differed between the two nets.

The euphausiid data complement results on larval fishes that led to adoption of the Bongo as the standard CalCOFI net, replacing the 1-m net.

RESUMEN

Se determinaron las abundancias de doce especies de eufáusidos de unos lances de plancton diseñados para comparar la capacidad de captura de una red cónica de apertura de 1-m con una brida de remolque anterior, y un muestreador Bongo sin brida con redes de apertura o de 60 o de 71 cm. Los arrastres repetidos consistían de arrastres consecutivos de la red de 1m y la Bongo, remolcadas oblicuamente a una profundidad de 210 m. Debido a que muchos eufáusidos migran a considerable profundidad durante el día, se usaron muestras tomadas de noche para determinar la eficacia relativa de las redes.

Para cada especie, se determinaron las diferencias entre las abundancias promedias de las muestras de la Bongo y de la red de 1 m. Se compararon las abundancias a cada intervalo de 1 mm en la longitud del cuerpo de la larva. Las larvas de las muestras de la red de 1 m eran más abundantes. La red Bongo retuvo mejor a los juveniles y adultos. Había poca diferencia entre los números totales para la mayoría de las especies.

Después de la fase larval la proporción de captura por la Bongo a la captura por la red de 1 m generalmente incrementaba con la longitud del cuerpo de la larva hasta llegar casi al tamaño mínimo. Los muestreos por medio de la Bongo resultaron en mayores estimaciones de biomasa. Para las dos especies en que se analizaron por separado a los machos y las hembras, las proporciones de los sexos diferían entre las dos redes.

Estos datos de eufáusidos complementan los estudios sobre peces larvales, cuyos resultados causaron que se reemplazara la red de 1 m con la Bongo como la red estándard de CalCOFI.

INTRODUCTION

Among active zooplankters such as euphausiids, more individuals are expected to swim away from than toward the path of an approaching tow net because nets produce visual and pressure signals. Aron (1962) discussed the many gear-dependent problems of sampling the macroplankton, of which adult euphausiids are a conspicuous, often predominant part. The modest body of data relating to net avoidance has been critically analysed by Clutter and Anraku (1968), who concluded that, despite contradictory evidence, avoidance occurs among many organisms designated as plankton.

Avoidance is to be expected when a towing bridle is positioned in front of the mouth of a net, as in the 1-m ring net that was in use by CalCOFI during 1950-76 (Ahlstrom 1952). This has led to the design of samplers such as the Bongo net (McGowan and Brown 1966) in which the tow line extends upward rather than forward from the mouth of the net. A measure of avoidance, however relative, will be made here by comparing catches of euphausiids from these two nets.

Mackintosh (1934), observing from the deck of a ship, first reported that *Euphausia superba* moves rapidly away from an approaching plankton net. Effectiveness of an avoidance reaction must vary with

[Manuscript revised 8 May 1981.]

the speed at which a net is towed, even assuming the same filtration efficiency at different speeds. Hansen (1960) showed that in the North Sea more adult euphausiids are captured per unit volume of water by a high-speed net of small mouth width than by a slow, larger Hensen net. However, Tranter (1966), varying tow speed between 0.4 and 4.0 knots (21 and 210 cm/second), caught fewer euphausiids at higher speeds. Aron and Collard (1969) found that 10-18-mm specimens of three species of euphausiid were in equal numbers in nighttime Isaacs-Kidd midwater trawl tows comparing towing speeds of about 2 and 4 knots (105 and 210 cm/second).

In the present comparison, the two nets are towed at nearly equal speeds, 1.5-2.0 knots (75-105 cm/second).

Effects of size of net mouth were discussed by Aron (1962). Adult euphausiids dominated catches obtained by an Isaacs-Kidd midwater trawl but were rare in samples from the same area from a much smaller Clarke-Bumpus net. Neither of these nets have bridles extending directly forward from the mouth. However, no differences were found between euphausiid abundances sampled by bridled nets of 1.0- and 0.45-m mouth widths (Brinton 1962a) or among nets having mouth areas of 0.5, 0.25, and 0.05-m^2 (Tranter 1966). Conversely, McGowan and Fraundrof (1966) found clear differences between abundances of euphausiids from a largest net (mouth width of 1.4-m) and smallest net (0.2 m) of a six-net array but not between nets of more similar size. They also reported no differences in euphausiid species composition among the samples from the net-size comparison series. Sands (1978) reported that a Longhurst Frame of 0.09-m^2 mouth area (the frame and net of a Longhurst-Hardy Plankton Recorder; Longhurst et al. 1966) sampled most groups of plankton in a Norwegian fjord as well as or better than a Beyer Low-Speed Midwater Trawl of 1-m^2 mouth area, with the notable exception of the large euphausiid *Meganyctiphanes norvegica*.

For the present analysis, samples were obtained both from series in which nets were towed alternately during a period of several hours and from isolated pairs of tows. P.E. Smith of the National Marine Fisheries Service was particularly instrumental in initiating this net-comparison study and has demonstrated (unpublished data) that anchovy larvae of greater than about 12-m length are significantly better sampled by the Bongo than by the 1-m net.

Like fish larvae, euphausiid crustaceans in the size range of about 5-25-mm body length are particularly active components of assemblages sampled by these plankton nets. The data are used to compare length-frequency (LF) distributions of euphausiids obtained by the two methods of sampling. Smith's analysis of fish larvae in the 1975 samples, together with the results presented here on euphausiids, have already led to adoption of the Bongo net for standard use in CalCOFI plankton surveys. It would be useful to know whether or not correction factors could be appropriately applied to estimates of euphausiid abundance obtained using the 1-m net during 1950-76 (Brinton 1967b, 1973, 1976; Brinton and Wyllie 1976).

METHODS

The samples are from two periods.

1) In January and July of 1975, collections were made with a "Marmap" Bongo of 0.6-m mouth width towed alternately with a CalCOFI ring net of 1.0-m mouth width (Figure 1). Both nets were of 333-μm mesh width. The same type of digital flowmeter was used in both nets. At each of three localities in the California Current, a daylight series consisting of five tows with each net was followed by a similar nighttime series. Tows were oblique to a depth of 210 m. During each 12-hour period of sampling, the ship followed a drogue positioned at 10-m depth. The northernmost locality (Figure 2) was near 35°N, 122°W, off central California within the cold-water regime of the current (CalCOFI Station 73.60 for winter series; Station 70.60 for summer series). The more southerly, warm-water localities were 30°N, 118.5°W (Station 103.60) and near 25°N, 114°W (Station 137.50, winter series; Station 133.46, summer series), both off Baja California.

2) From December of 1977 through August of 1978, during the course of seven CalCOFI survey cruises, a total of 61 pairs of samples—one sample from the 1-m ring net and one from a Bongo net of 0.71-m mouth width—were obtained at numerous stations off California and Baja California.

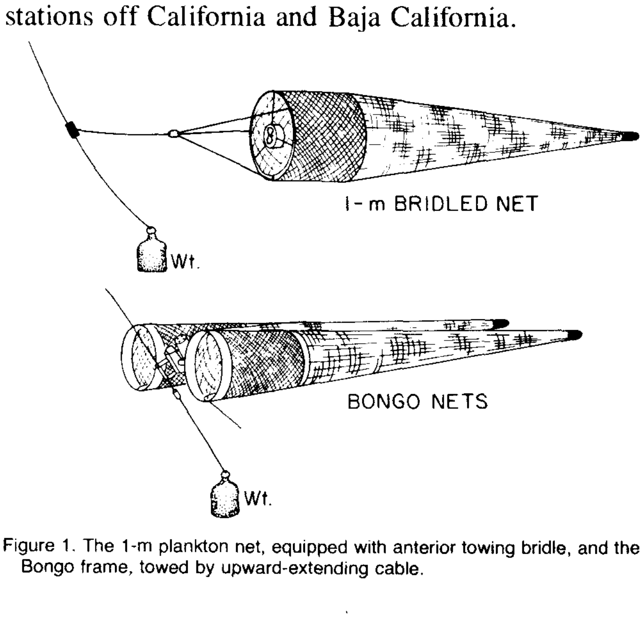

Figure 1. The 1-m plankton net, equipped with anterior towing bridle, and the Bongo frame, towed by upward-extending cable.

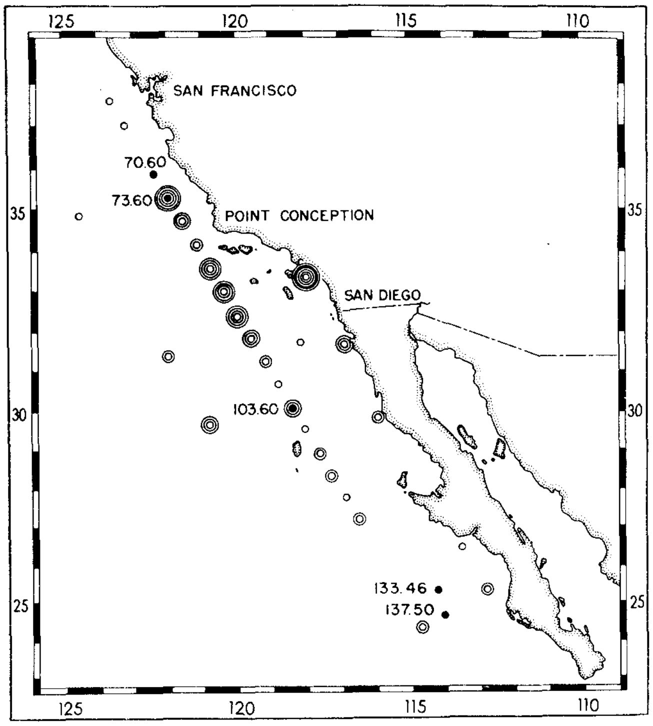

Figure 2. Localities in the California Current at which the nighttime tows used in this comparison of the Bongo and 1-m net were made. At the position of each solid circle, there were six nighttime and six daytime pairs of replicate tows in either January or July 1975. An open circle indicates a pair of tows from one of the CalCOFI Cruises during 1977–78, and concentric circles represent pairs from two or more of the cruises.

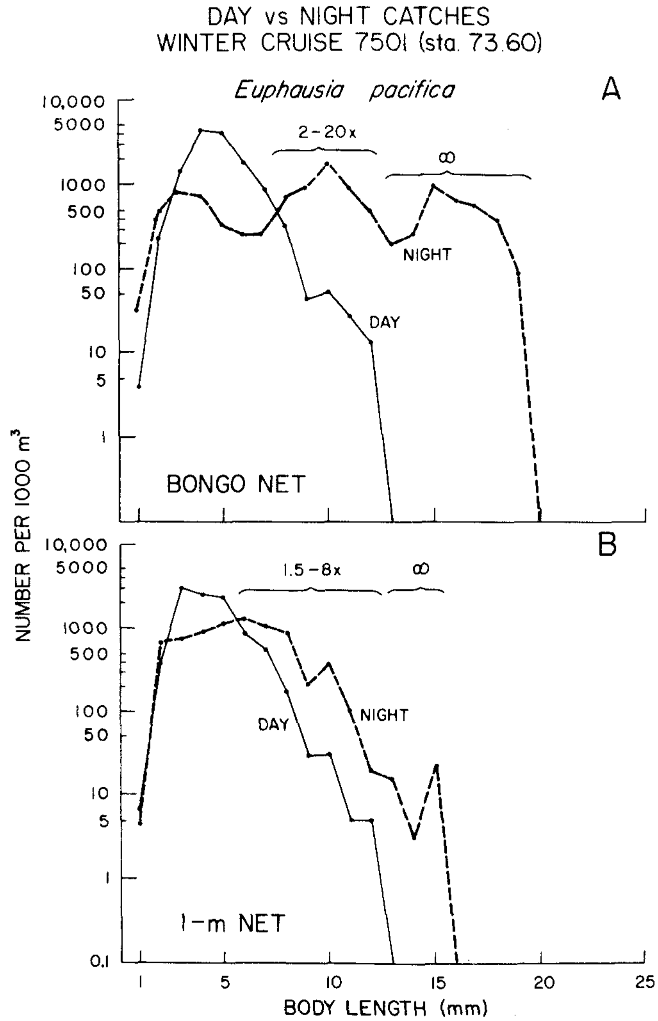

Figure 3. Length-frequency (LF) distributions of *Euphausia pacifica* from the day-night series of January, 1975, in which Bongo and 1-m net tows were alternated, yielding six daylight and six nighttime pairs of samples. Each LF curve is the mean of the six catches. Day and night abundances: A. from Bongo net; B. from 1-m net. Night/day catch ratios are indicated.

The present analysis deals only with nighttime pairs of samples, except in the case of the abundant *Euphausia pacifica*: the 1975 daytime data for this species is included to illustrate the character of day-night differences in abundance within the 0-210-m layer. Such differences reflect a combination of the effects of vertical migration and avoidance. Samples obtained at night are generally more useful for estimating euphausiid abundances because all growth stages are then in the upper layer of the ocean.

Samples were subsampled using the Folsom splitter. Analysis of the relatively large 1975 samples were of 1/32 fractions. The 1977-78 samples were examined following the method described in Brinton (1979), in which progressively larger fractions of a sample are examined for the increasingly rarer sizes of a given euphausiid species.

Twelve species were considered to be sufficiently abundant in enough of the paired samples to permit combining data among stations. A mean length-frequency distribution of a species was determined from all catches from each type of net.

Euphausia pacifica and *Nematoscelis difficilis* were particularly abundant in the mid-part of their ranges off central California, sampled during the winter and summer series of 1975. Therefore, these two species will be examined in most detail.

RESULTS

Day versus Night Catches, **Euphausia pacifica**

The mean length frequency(LF) for the five nighttime Bongo samples from the central California locality, Station 73.60, in January (Figure 3A) extends from 1-mm larvae through 19-mm adults. The five daytime Bongo tows captured specimens only in the range of 1-12 mm. In the 8-12-mm size range, nighttime abundances were 2 to 20 times greater than daytime estimates. These larger nighttime catches of *E. pacifica* may be attributed (1) to the deeper (>210-m) daytime levels of some large juveniles and adults due to vertical migration (Brinton 1967a) and (2) to differential day-night avoidance of the net by those 8-

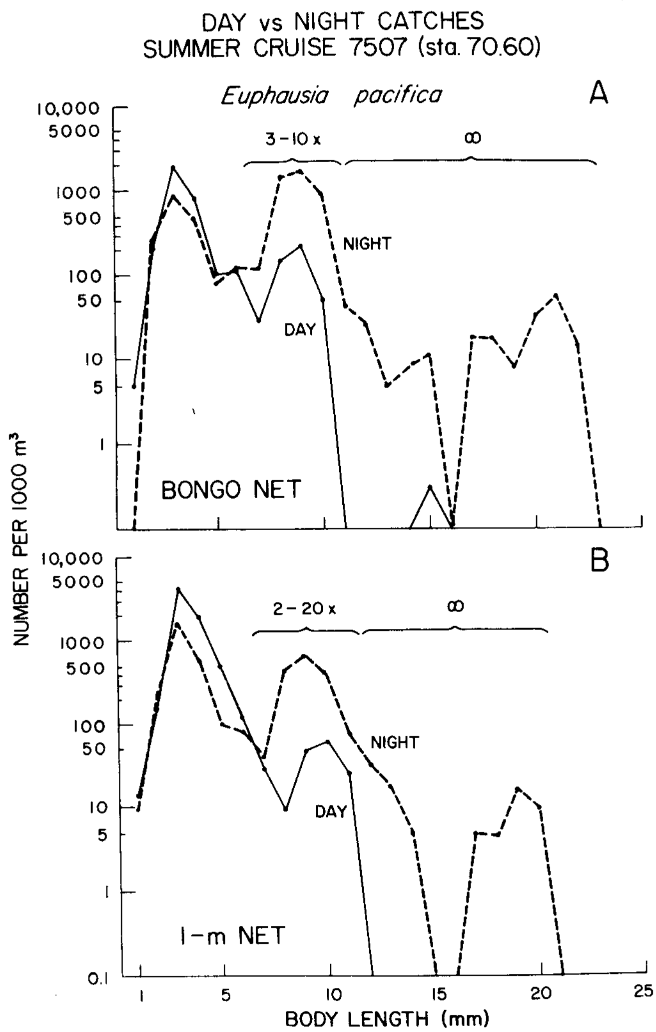

Figure 4. Length-frequency (LF) distributions of *Euphausia pacifica* from the day-night series of July, 1975, in which Bongo and 1-m net tows were alternated, yielding six daylight and six nighttime pairs of samples. Each LF curve is the mean of the six catches. Day and night abundances: A. from Bongo net; B. from 1-m net. Night/day catch ratios are indicated.

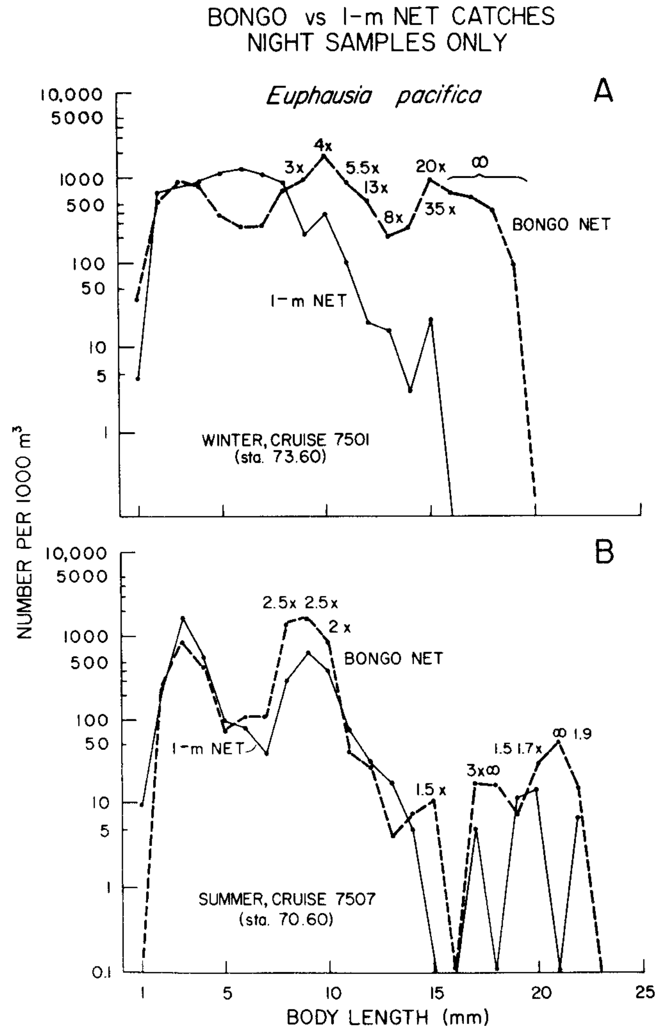

Figure 5. Mean LF distributions of *Euphausia pacifica* from nighttime series: A. January 1975; B. July 1975, during which Bongo and 1-m net tows were alternated. Bongo/1-m-net catch ratios are indicated at body lengths where Bongo catch was the greater.

12-mm individuals that were above 210-m at all times. On the other hand, small 3-7-mm *E. pacifica* were better sampled by day than by night.

Like the Bongo net, the 1-m net caught 1-12-mm *E. pacifica* in the daytime (Figure 3B), but only 1-15-mm at night, compared to 1-19-mm for the Bongo.

In the summer-daytime samples (Figure 4), *E. pacifica* of 1-10 mm or 1-11 mm were caught by the 1-m net, compared to 1-12 mm by both nets in the winter-daytime samples. However, the summer-nighttime Bongo samples showed that the population then included specimens of up to 22 mm. The day-time sampling by both nets is relatively inefficient for 7-10-mm or 7-11-mm *E. pacifica* and is essentially nil for larger sizes. As in the winter, the summer sampling of 3-6-mm specimens was more effective in the daytime than at night.

Bongo versus 1-m Net, Nighttime, E. pacifica

Relative efficiencies of the Bongo and 1-m nets become particularly evident when the nighttime catch curves are compared directly (Figure 5).

During the winter series (Figure 5A), at body lengths >8 mm, a nearly direct relationship was seen between body length and capability of *E. pacifica* to avoid the 1-m net: at 9 mm, the Bongo catch was three times that of the 1-m net; at 15 mm it was 35 times greater, and for sizes greater than 15 mm, avoidance of the 1-m net was total. A seasonal difference in the response of *E. pacifica* to the net may be inferred from an apparently greater capacity of large juveniles and adults to avoid the 1-m net during the winter series. The summer curves for the two nets (Figure 5B) were more nearly the same through the size range of 2-14 mm, and catches of larger adults

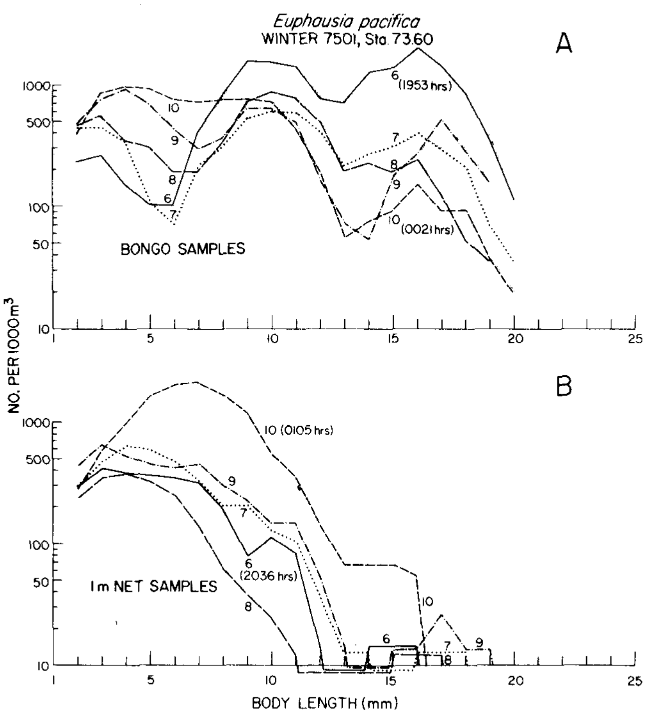

Figure 6. LF distribution of *Euphausia pacifica* from nighttime pairs of net-comparison tows, numbered 6 to 10, comprising the January (winter) 1975 series: A. Bongo; B. 1-m net samples.

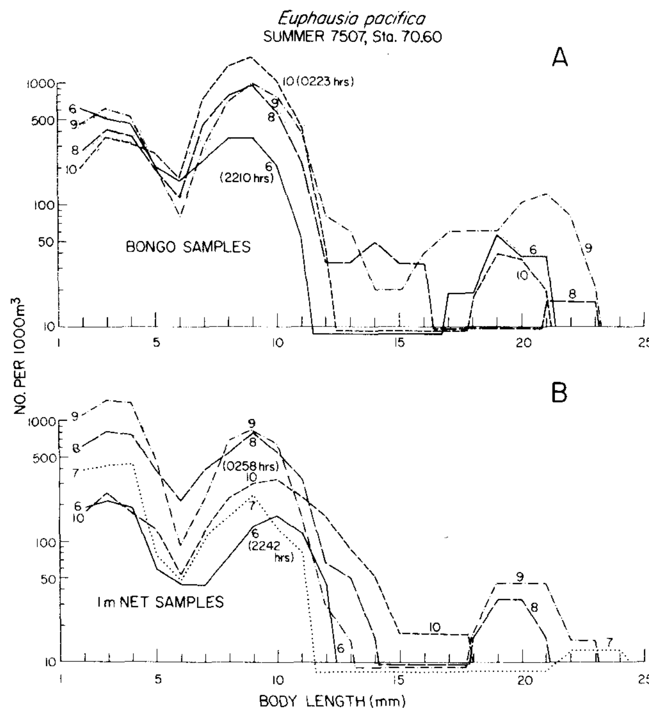

Figure 7. LF distribution of *Euphausia pacifica* from nighttime pairs of net-comparison tows, numbered 6 to 10, comprising the July (summer) 1975 series: A. Bongo; B. 1-m net samples. Bongo sample Number 7 was lost.

usually differed by factors of <3. However, because the larger *E. pacifica* were 20 times more abundant in the winter than in the summer samples, the relative importance of season, population density, or other factors to avoidance capability are unclear from these samples alone.

The mean LF distributions in Figure 5 are based on the individual winter and summer samples in Figures 6 and 7. Of the three distinct modes in the curves representing the winter Bongo samples (Figure 6A), the one at 3-4 mm was also clear and of similar magnitude in four of the five 1-m net samples (Figure 6B). The mode at 9-11 mm was small in all 1-m net samples, discernible only as shoulder to a major mode. The mode at 14-18 mm appeared regularly in the 1-m net samples but as a low peak representing few individuals, compared to abundances of 100 to >1,000/ 1,000 m³ in the Bongo samples.

The summer Bongo series also recorded three modes (Figure 7A). Two were just as clear in the 1-m net samples (Figure 7B), though the 8-10-mm mode was based on abundances about one-half as great as those caught by the Bongo. The Bongo mode for large adults 18-22 mm in length was discernible in three of the five 1-m net samples.

Hourly Time Change in E. pacifica *Population Structure*

The five winter-nighttime Bongo samples obtained during 1953-0021 hours (Figure 6A) show (1) near constancy with time in numbers of the 2-3-mm larvae and 7-12-mm juvenile-adults; (2) an increasing number of 4-6-mm specimens, until a factor of 10 separates the last tow, Number 10, from the first, Number 6; and (3) a decrease in numbers of 13-mm adults during the same 4½-hour period.

Bongo and 1-m net sampling alternated at half-hour intervals. Nevertheless, the Bongo curves are more similar among themselves than to any from the 1-m net (Figure 6B). Of the latter, Numbers 6-9 were most alike, whereas the final tow of the night, 1-m net Number 10, caught relatively numerous 4-16-mm specimens, much as the first tow of the night, Bongo Number 6, had caught particularly numerous specimens of 9-20 mm.

Effects of Bongo Mouth Width on Catch of E. pacifica

The 1975 winter and summer series compared the 1-m net with Bongo nets of 60-cm mouth width. The December 1977-August 1978 comparisons employed Bongo nets of 71-cm mouth width, designed so that the combined mouth area of the tandem nets equals the 0.785-m² mouth area of the 1-m net. An analysis to determine whether there is a difference in effectiveness—versus the 1-m net—between the two sizes of Bongos is limited by the substantial difference (Figure 5) between results of the winter and summer net-comparison series of 1975, both of which employed the smaller Bongo. During the winter series, the

Bongo caught significantly more *E. pacifica*, in relation to the 1-m net catch, than during the summer. This difference is still evident when the most atypical sample of each five-sample winter set (Figures 6A,B; Bongo sample Number 6 and 1-m-net sample Number 10) is omitted from the computation of mean LF distributions (Figure 8A). Therefore, combining 1975 winter and summer data on 60-m Bongo versus 1-m net appears unjustified for purposes of comparison with the 1977-78 data on 71-cm Bongo versus 1-m net. Such combining of data could have prompted the inference that the smaller Bongo is more efficient than the larger.

Nevertheless, the summer 1975 data for small Bongo and 1-m net (Figure 8B) closely resemble the 1977-78 data for large Bongo and 1-m net (Figure 8C, all seasons combined), when ratio of Bongo catch to 1-m net catch is plotted as a function of body length of *E. pacifica* (Figure 8D). In both series, the greatest relative Bongo net efficiency is at body lengths of 6-11, 14-18, and 21-22 mm. The magnitude of the ratios is similar. Only the anomalous data from the 1975 winter deter a conclusion that the different sized Bongo nets are equally effective samplers of *E. pacifica*.

Effects of Season, the 1977-78 Data, **E. pacifica**

The better ability of juvenile and adult *E. pacifica* to avoid the 1-m net during the 1975 winter series (Figure 8A), compared with the summer (Figure 8B), prompts examination of seasonal aspects of data from the 1977-78 period. Bongo/1-m-net catch ratios show the spring and summer curves to be roughly parallel (Figure 9).

Although represented as a mean of only eight stations of paired net tows, the 1977-78 winter data differ from that of the other seasons, as in 1975. In this instance, however, the anomaly in the winter data is the near equality of the two nets as catchers of juveniles and adults. In addition, 1-5-mm larvae were better sampled by the 1-m net by factors as great as 4-8 during the winter, though absolute numbers of these larvae were then low compared with spring and summer. Reasons for these inconsistencies in the winter data are not evident.

Male, Female, and Life-Phase Abundances versus Net Type, **E. pacifica**

Males and females are plotted separately (Figure 10A) in the adult segments of catch curves expressing mean LF distributions for the net-comparison stations at which *E. pacifica* occurred. The Bongo net tended to catch more males than females, and the 1-m net caught relatively more females.

Because there were more adult *E. pacifica* in the

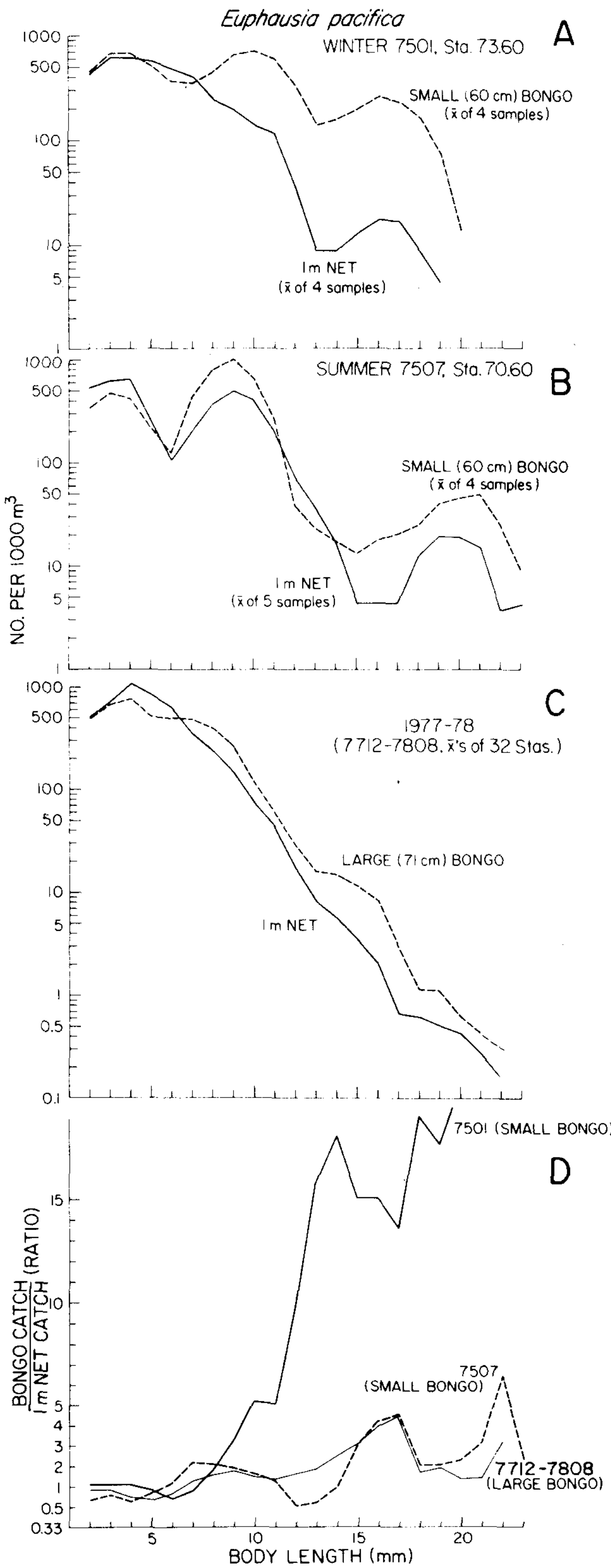

Figure 8. Mean LF distributions of *Euphausia pacifica* (3-point running averages): A. winter 1975 series, comparing 60-cm Bongo catches with 1-m net catches, *omitting aberrant pairs Numbers 6 and 10 (Figure 6)*; B. summer 1975 series, also comparing 60-cm Bongo with 1-m net; C. 1977–78 pairs of tows, comparing 71-cm Bongo with 1-m net; D. Bongo/1-m-net catch ratios for the above.

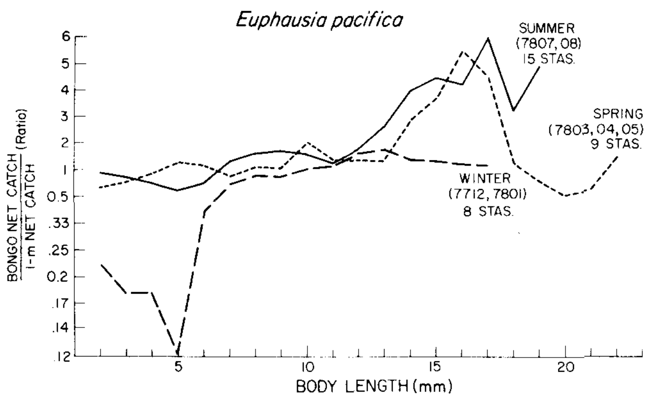

Figure 9. Mean Bongo/1-m-net catch ratios for *Euphausia pacifica* comparing winter, spring, and summer net-comparison sampling during 1977–78.

Bongo samples, it is supposed that the Bongo data provide the better description of a real population, in which males are narrowly in the majority, particularly in the range of 13-20-mm body length.

It appears unlikely that the apparent male predominance in the Bongo samples is due to a better capability of females to avoid that net. The 1-m net with its anterior bridle presents the more obvious stimulus to avoidance by adult euphausiids, and it caught more females than males.

For males, the ratio of Bongo catches to 1-m net catches increases during adulthood from 11 mm to 17 mm body length (Figure 10B). For females, it increases during 13 mm to 18 mm. After 17 or 18 mm, this ratio decreases sharply, as does the number of individuals.

When the Bongo/1-m-net catch ratio is changed to a logarithm (Figure 11), straight lines may be fitted to segments of the curve representing that ratio plotted as a function of body length. The individual segments have different slopes and appear to relate to life phases.

The 1-m net is the better catcher of larvae, and the ability of *E. pacifica* to avoid the Bongo increases during larval development. This trend is reversed at the start of the postlarval period. By 7-mm body length, the Bongo has become the better catcher. There is a diminished rate of increase in catch ratio during juvenile growth from 7 to 11 mm, followed by an increased rate.

At 17-mm body length, the Bongo is catching an average of 16 times more males and eight times more females than the 1-m net. After 17-18 mm the ratios decrease. By 21 mm the Bongo catch of both sexes is only three times the greater.

A measure of the statistical significance of the larger average catches of 1-6-mm *E. pacifica* by the 1-m net (Figure 10A) is the following: 150 pairs of Bongo/1-m net abundances contributed to the mean abundances at the six 1-mm body-length increments, and in 98 (65%), abundance in the 1-m net sample was the greater.

Significance of the larger average catches of 7-21-mm *E. pacifica* by the Bongo net (Figure 10A) is seen in the same way: 407 pairs of Bongo 1-m net

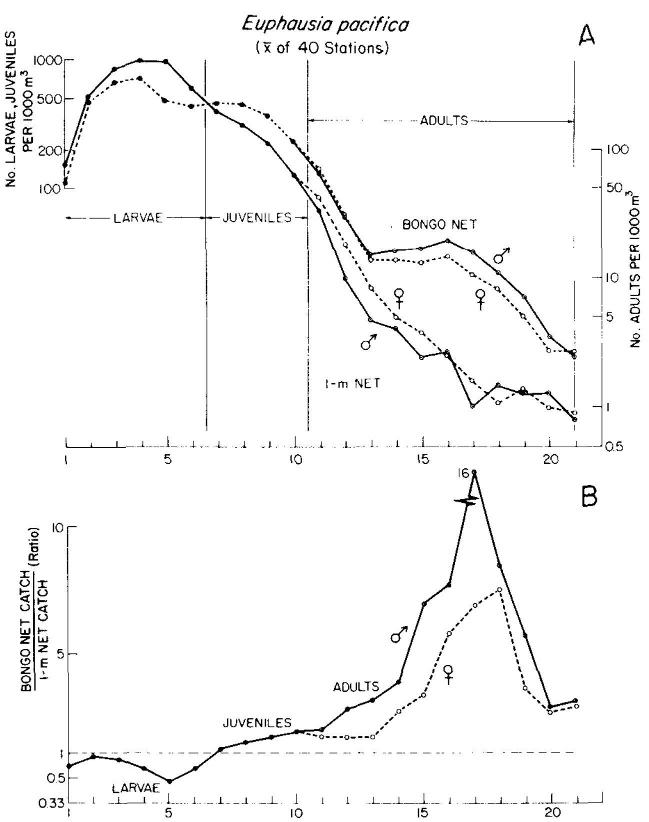

Figure 10. A. LF distributions of *Euphausia pacifica* (3-point running averages), comparing mean of all 1975–78 Bongo catches with mean of 1-m net catches. Adult males and females are separated. B. Bongo/1-m-net catch ratios for abundances shown in A.

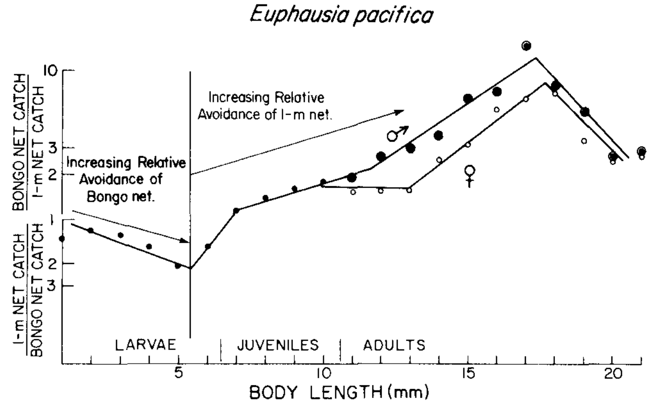

Figure 11. Catch ratios for *Euphausia pacifica*, logarithmic scale, relating 1975–78 mean distribution from Bongo catches with mean from 1-m net catches.

abundances contributed to the 15 pairs of mean abundances, and in 287 (71%), abundance in the Bongo sample was the greater.

Nematoscelis difficilis

Nematoscelis difficilis is more broadly distributed than its cool-water associate, *E. pacifica*, in the California Current (Brinton 1962b, 1967b). It was present in substantial numbers in 56 of the 90 net-comparison pairs of tows compared to 40 for *E. pacifica* but was usually at lower density when the two species co-occurred.

Larvae and small juveniles (to 6-mm length) of *N. difficilis* were better sampled by the 1-m net than by the Bongo (Figure 12 A,B). The Bongo/1-m-net catch ratio decreased somewhat during the course of the larval phase (Figure 12B), as in *E. pacifica*, before beginning an unsteady increase into the juvenile phase. The sharp decrease in abundances measured by both nets during development from 3 to 10 mm almost certainly represents a period of rapid growth associated with increasing ability to avoid the 1-m net.

Mean abundance increases with body length between 10 and 15 or 16 mm, indicating slowed growth during the late juvenile phase and the onset of maturity. Bongo catches are three times the greater during this period.

After about 16-mm body length there is a trend in both sexes toward increasing capability to avoid the 1-m net. This coincides with diminishing numbers of individuals at given body lengths due to increasing mortality, reaccellerated growth, or both. Improved ability to avoid both nets may also play a role. The smallness of numbers of individuals upon which the ratios for largest sizes are based reduces their significance.

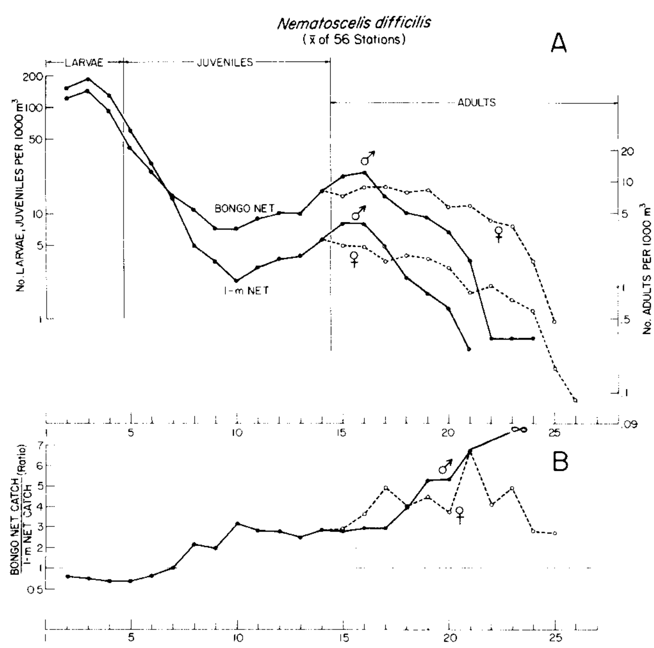

Figure 12. A. LF distributions of *Nematoscelis difficilis* (3-point running averages), comparing mean of all 1975-78 Bongo catches with mean of 1-m net catches. Adult males and females are separated. B. Bongo/1-m-net catch ratios for abundances shown in A.

The maximum length reached by female *N. difficilis* is known to be about 2 mm more than the male. Sampling by the 1-m net would have indicated a greater disparity, 26 mm for females and 21 mm for males. However, the Bongo caught some males as large as 24 mm.

Statistical significance of the larger average catches of 1-6-mm *N. difficilis* by the 1-m-net (Figure 12A) may be estimated from the following: 211 pairs of Bongo/1-m-net abundances contributed to the mean abundances at the six 1-mm length increments, and in 135 (65%), abundance in the 1-m-net sample was the greater.

Significance of the larger average catches of 7-25-mm *N. difficilis* by the Bongo net is seen in the same way: 464 pairs of Bongo-1-m net abundances contributed to the 26 pairs of mean abundances, and in 334 (72%), abundance in the Bongo sample was greater.

The bimodal shape of the LF curves (Figure 12A) closely agrees with the shape of an unpublished catch curve for *N. difficilis* representing an average of data from many monthly CalCOFI cruises extending from 1953 to 1958. Thus, this bimodal distribution seems to be the persisting population structure in this species. It reflects alternating phases of rapid and slowed growth.

The two modes appeared in exaggerated form in LF curves representing the 1975 winter and summer series off central California (Figure 13 A,B). The curve combining those Bongo/1-m-net catch ratios peaks particularly sharply at 8-11-mm body lengths.

As with *Euphausia pacifica*, the combined data on *N. difficilis* for all of 1977-78 (Figure 13 C,D) indicate less disparity between Bongo and 1-m-net catches than does the 1975 data. A modest mode in the catch ratio curve was nevertheless distinguishable at 8-10 mm, corresponding with the extreme mode in the 1975 data.

Euphausia eximia *and* E. gibboides

Euphausia eximia and *E. gibboides* are two large species inhabiting, respectively, more southern and more offshore waters of the California Current than do *E. pacifica* and *Nematoscelis difficilis*, while also overlapping parts of the range of those cool-water species. At night, *E. eximia* migrates up into the mixed layer, and *E. gibboides* only up into the ther-

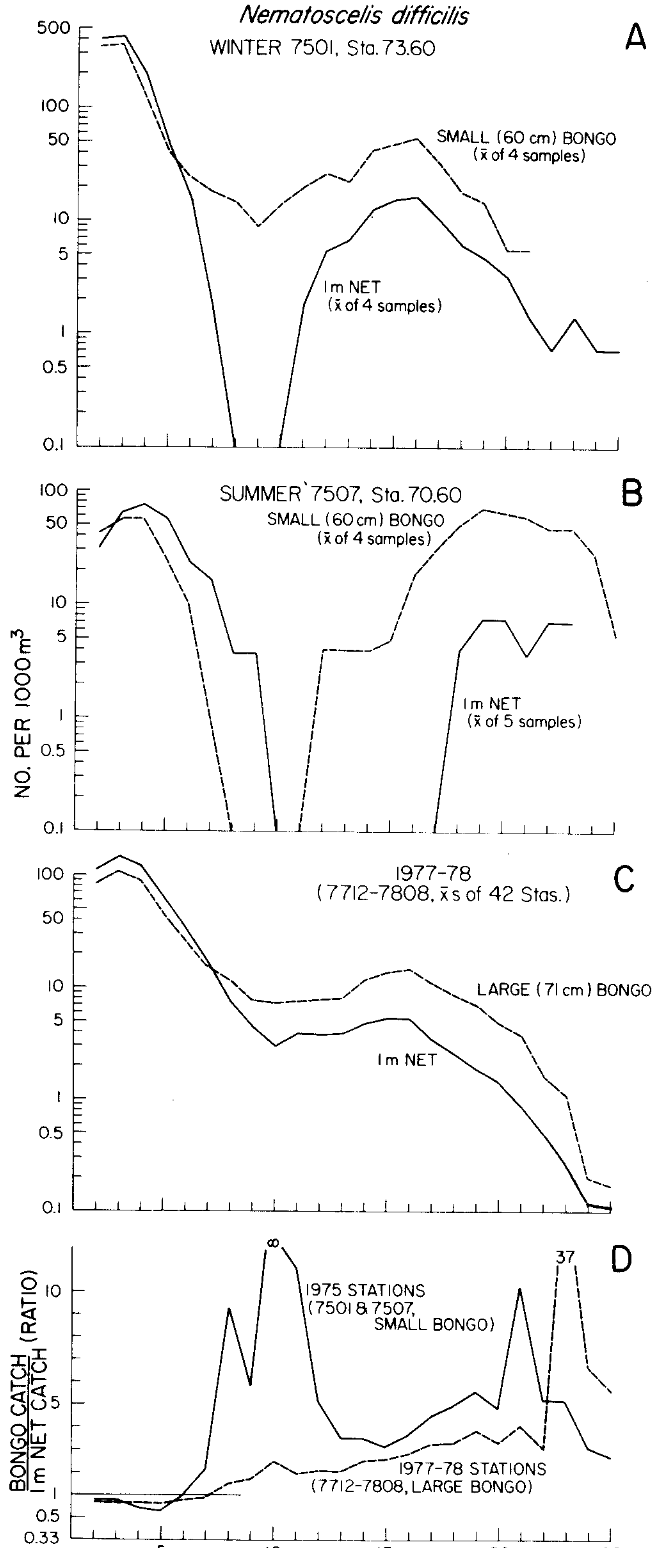

Figure 13. Mean LF distributions of *Nematoscelis difficilis* (3-point running averages): A. winter 1975 series, comparing four similar 60-cm Bongo catches with four 1-m net catches; B. summer 1975 series, also comparing 60-cm Bongo with 1-m net; C. 1977–78 tows, comparing 71-cm Bongo with 1-m net; D. Bongo/1-m net catch ratios for the combined 1975 data and the combined 1977–78 data.

mocline. The 0-210-m depth of sampling encompasses these nighttime levels.

As with *E. pacifica* and *N. difficilis*, larvae of *E. eximia* and *E. gibboides* were caught better by the 1-m net (Figure 14 A,B). The Bongo was the more effective catcher of adult *E. eximia* by as much as 3.5 times at 18-19 mm and 24-25 mm.

The Bongo was the more effective net for catching *E. gibboides* juveniles and adults. As with *E. eximia*, the body lengths at which the Bongo was relatively most effective were near 17-19 mm and again at maximum size, 24-25 mm in this species.

Euphausia hemigibba and *E. recurva*

These are smaller species than the above. Both are characteristic of the offshore part of the California Current, though they extended more inshore than usual during the 1977-78 period of sampling (Brinton 1981).

Euphausia hemigibba larvae were in nearly equal numbers in the Bongo and 1-m net catches, with the 1-m-net a little more effective for 3-4-mm sizes (Figure 15A). Juveniles and large adults were caught better by the Bongo by factors of 3 to 4, though mid-

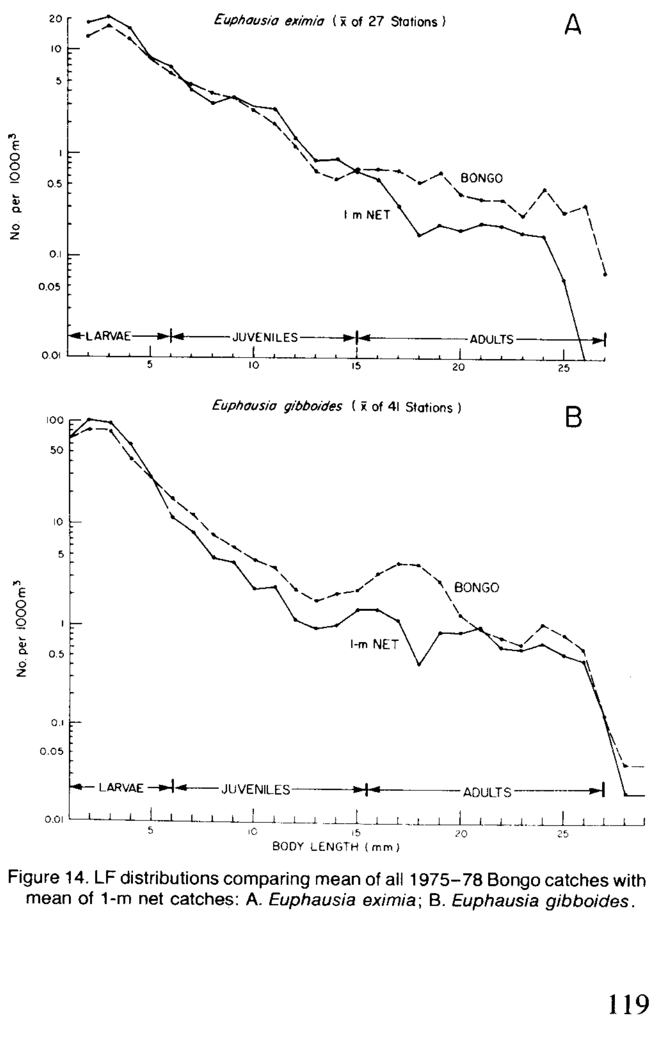

Figure 14. LF distributions comparing mean of all 1975–78 Bongo catches with mean of 1-m net catches: A. *Euphausia eximia*; B. *Euphausia gibboides*.

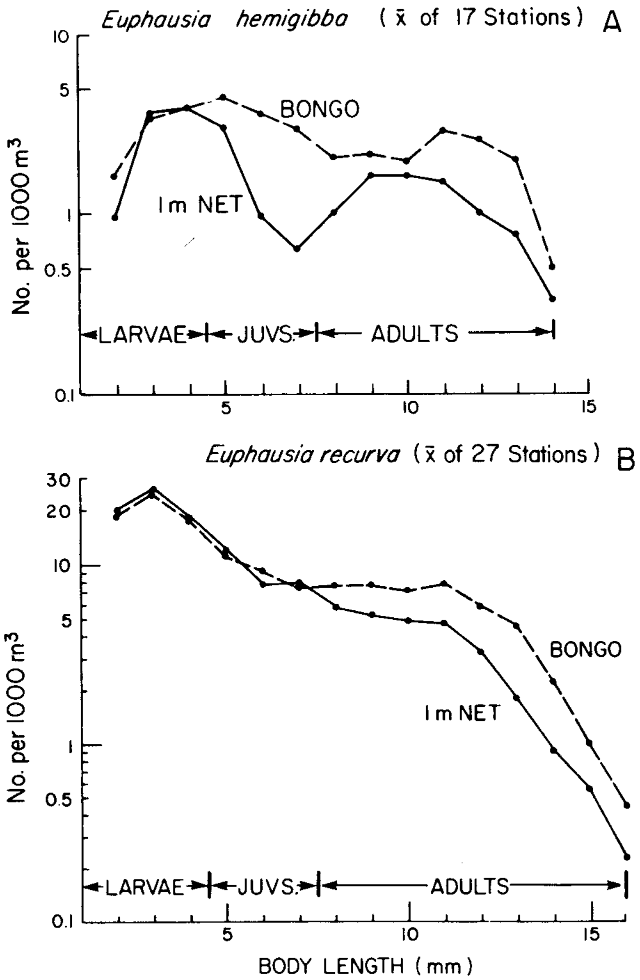

Figure 15. LF distributions comparing mean of all 1975–78 Bongo catches with mean of 1-m net catches: A. *Euphausia hemigibba*; B. *Euphausia recurva*.

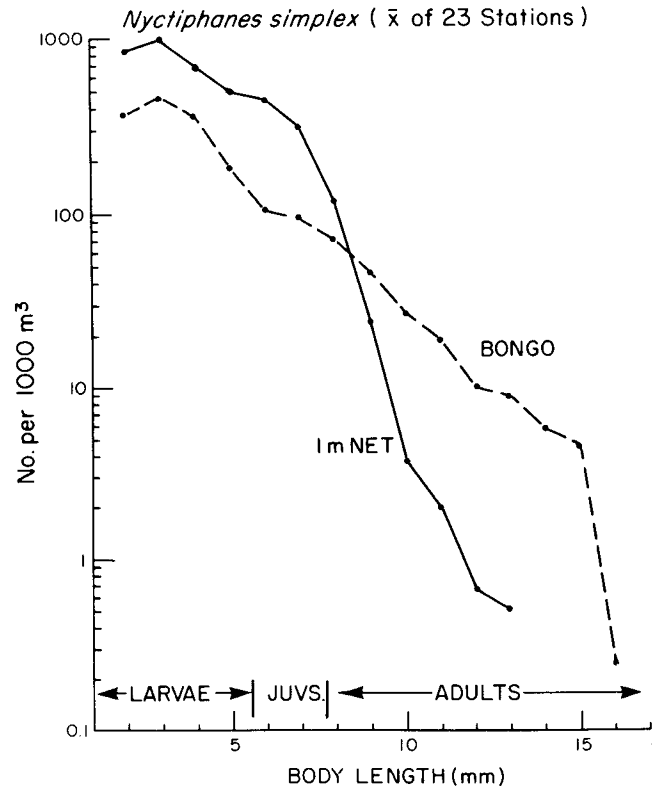

Figure 16. LF distributions of *Nyctiphanes simplex*, comparing mean of all 1975–78 Bongo catches with mean of 1-m net catches.

adults of 9-10-mm length were almost as numerous in the 1-m net catches.

Euphausia recurva larvae were barely caught better by the 1-m net (Figure 15B). Bongo catches of adults were 1.5 times (at 8-mm length) to 2.5 times (at 13-14 mm) greater than those of the 1-m net.

Nyctiphanes simplex

N. simplex is frequently abundant in coastal waters of southern California and Baja California. Its LF distributions showed particularly clear relationships between life phase and relative retention by the two nets (Figure 16). Larvae were better sampled by the 1-m net by a factor of 2 and juveniles by a factor of 4. During the course of adulthood, the Bongo became increasingly the better collector.

Thysanoessa spinifera

Like *Nyctiphanes simplex*, *Thysanoessa spinifera* is a coastal, even neritic, species. Its range generally extends farther north than that of *N. simplex*, though there is overlap, particularly along southern California.

In this large species, the larval phase, as indicated by incomplete telson development, extends to 8-mm body length, although antennae and pleopods assume the juvenile form by 6-mm length. The latter structural and functional changes also delineate the stage at which the Bongo becomes the more efficient means of capture. As a sampler of adults, the 1-m net yielded only a few specimens of 14-15-mm length, whereas the Bongo retained 13 times as many of that size, plus some as large as 21 mm.

Nematobrachion flexipes

N. flexipes is a large, sparse, widely-ranging, oceanic species having an unclear pattern of vertical migration, possibly swimming randomly through the mixed layer and thermocline, day and night (Brinton 1979). The Bongo is scarcely better than the 1-m net at capturing *N. flexipes* until this species has attained a length of 16 mm (Figure 17B). Thereafter, avoidance of the 1-m net was nearly complete, whereas the Bongo caught specimens up to 26 mm in length.

Thysanoessa gregaria, Stylocheiron affine *and* S. longicorne

These three small euphausiids occur throughout

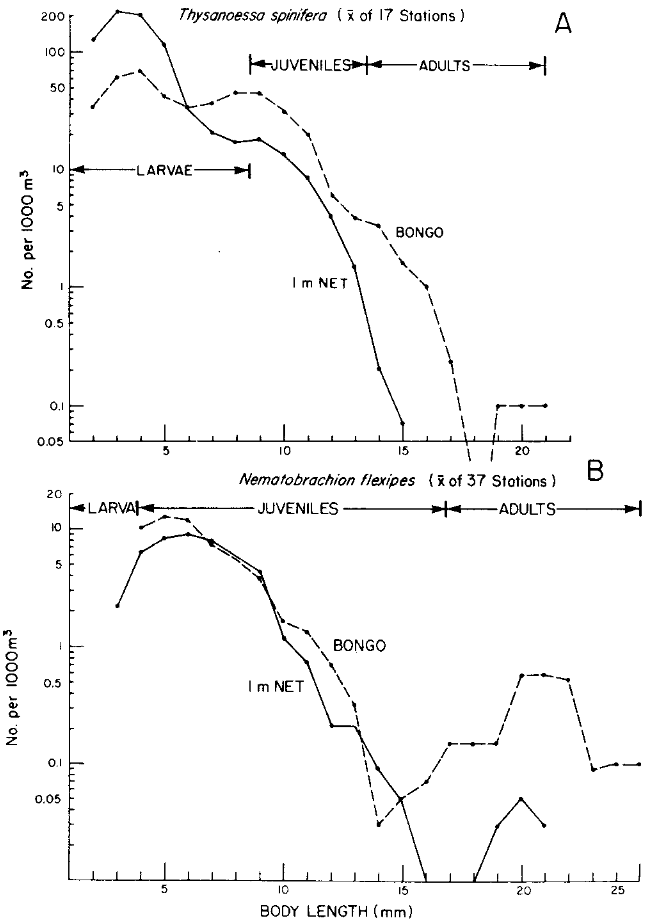

Figure 17. LF distributions comparing mean of all 1975–78 Bongo catches with mean of 1-m net catches: A. *Thysanoessa spinifera*; B. *Nematobrachion flexipes*.

much of the California Current. Unlike the other species here, all have depth ranges centered within the thermocline, day and night, in the deeper half of the 0-210-m layer sampled by our nets. The estimates of density of *Stylocheiron longicorne* may be the least accurate because this species tends to be deeper than *S. affine* and *Thysanoessa gregaria*, probably extending down to 250 or 300 m.

The three have been considered to be nonmigrators but with much stronger capacities for avoidance of nets in the daytime than at night in their mid-depth habitats (Brinton 1967a, 1979). This was construed as evidence of visual orientation to predators. During our nighttime comparative sampling, *T. gregaria* of 6-13-mm length were caught better by the Bongo net by a factor of 2. This value is much like the Bongo/1-m net-capture ratio for the approximately 6-13-mm juvenile phase of some of the larger species discussed above, e.g. *Euphausia pacifica* (Figure 10), which attained stronger avoidance capacity only beyond a length of about 13 mm, in early adulthood.

On the other hand, all sizes of the two *Stylocheiron*

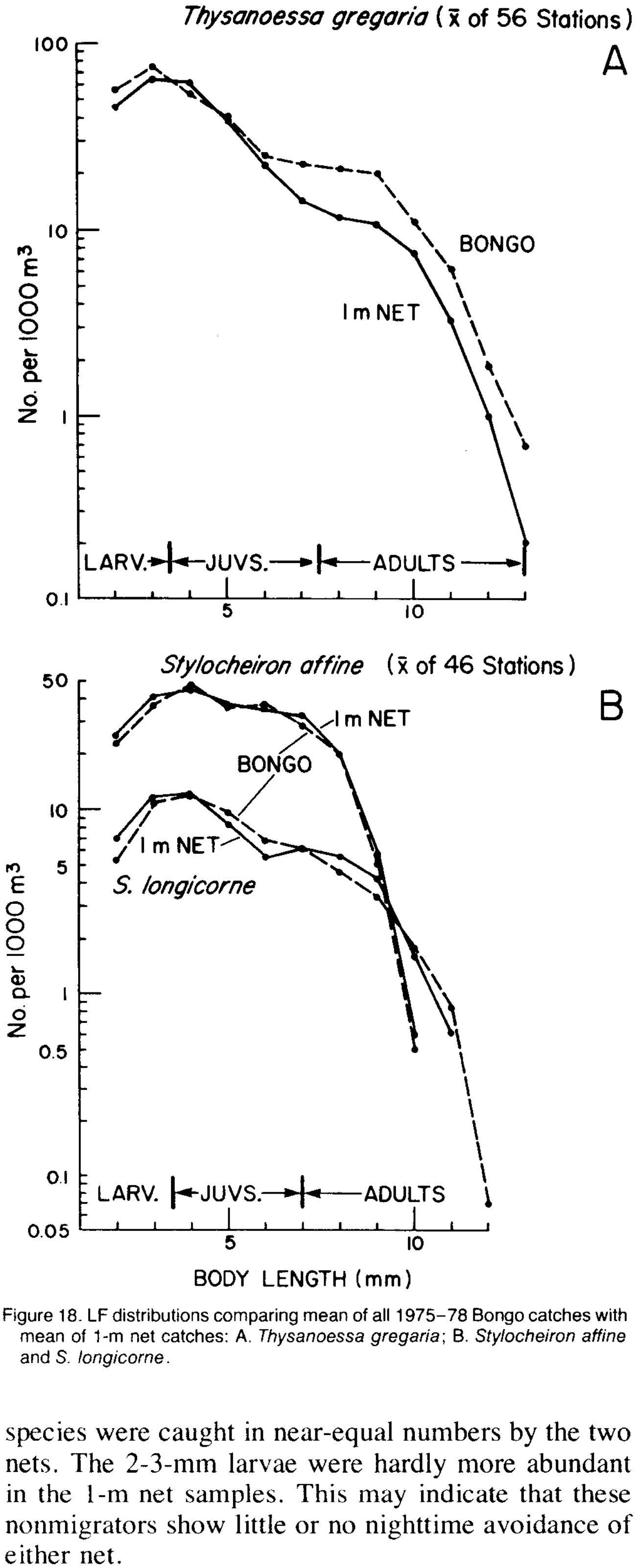

Figure 18. LF distributions comparing mean of all 1975–78 Bongo catches with mean of 1-m net catches: A. *Thysanoessa gregaria*; B. *Stylocheiron affine* and *S. longicorne*.

species were caught in near-equal numbers by the two nets. The 2-3-mm larvae were hardly more abundant in the 1-m net samples. This may indicate that these nonmigrators show little or no nighttime avoidance of either net.

SUMMARY AND DISCUSSION

Euphausiid abundances were measured by replicate tows, in which a tow with a Bongo net was followed by a tow with a 1-m ring net. Significant characteristics of the nets are the anterior bridle on the 1-m net, compared with the bridleless Bongo, and the large mouth of the 1-m diameter ring net compared with 60-cm and 71-cm for the two types of Bongos used. However, the present set of samples are insufficient to relate differences in catching capacity to these characteristics. Comparable samples would be required from a bridleless 1-m net and from a Bongo-sized net with anterior bridle. Generalities emerging from the comparisons are the following:

1. Larval euphausiids, on the average, appear to be at higher density when sampled by the 1-m net than by the Bongo, though by a factor of less than 2 for most species.

2. Juveniles and, to a greater extent, adults of >13-mm body length are usually better sampled by the Bongo net, frequently by factors of 3 or more. Typically (Figure 19), the Bongo/1-m-net catch ratio peaks first during mid-adulthood and again at maximum size, though numbers are then becoming small.

3. Relative proportions of adult males and females differ between the Bongo and 1-m net samples.

4. Length-frequency histograms such as those averaging euphausiid population structure over a monthly period based on 1-m net tows (Brinton 1976) cannot reliably be amended by factors reflecting the greater average abundances of juveniles and adults found by Bongo sampling. However, species biomass estimates may be modified upward using Bongo/1-m-net ratios.

Larval Avoidance

The better catches of larvae by the 1-m net and of juveniles and adults by the Bongo may prove to be related to behavior that is characteristic of particular life phases. Such behavior should be amenable to experimental study. For example, in 10 of 11 species, mean LF curves indicate that larvae with, as yet, incomplete development of pleopods (swimming legs) are soewhat better sampled by the 1-m net than by the Bongo. In *Nematobrachion flexipes*, larvae with incomplete development of pleopods are smaller than about 3.5-mm and were not present in these samples. During much of larval development, euphausiids swim by means of antennae and do not yet engage in extensive vertical migration. The proportion of larvae able to avoid the Bongo net relative to the larger 1-m net increases during the larval phase in *E. pacifica* and *N. difficilis* (Figures 10B, 12B). Larvae may be relating to the *size* of the approaching net and less cued directionally by the approach of a net bridle. The smallest, least active larvae were found at the same abundance by the two kinds of net. With increasing body length, fewer larvae seem able to avoid the 1-m-net than the Bongo mouth with its greater perimeter-to-area ratio. That is, if larvae of a particular size are in the path of an approaching net and are capable of an avoidance reaction of a specific distance, there will be more such larvae, relative to the mouth area, within avoiding distance of the rim of a small net compared with a larger one. As larvae grow to 2- to 5-mm length, the extent of this avoidance reaction should increase, so that progressively smaller densities will be recorded by the Bongo, relative to the 1-m net, as is observed to be the case.

A reviewer of this paper has suggested that weakly swimming larvae might cease conspicuous activity upon sensing the approach of a predator. This could have the effect of increasing numbers of larvae near the leading bridle and cause overestimation of larval abundance.

Curiously, *E. pacifica* larvae were sampled at higher density by day than by night by both the Bongo and the 1-m net (Figure 3).

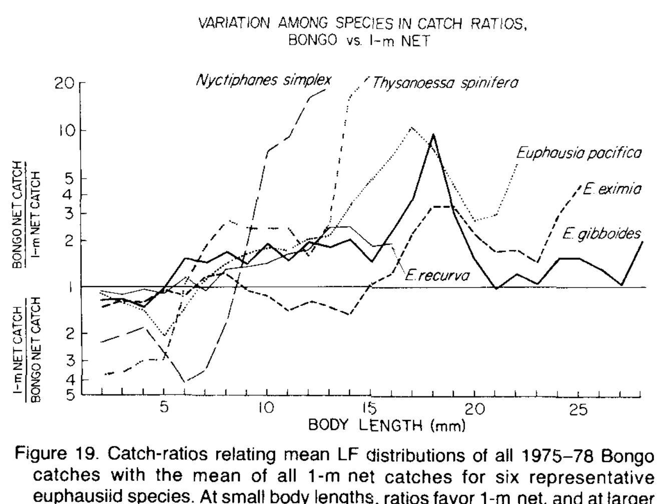

Figure 19. Catch-ratios relating mean LF distributions of all 1975–78 Bongo catches with the mean of all 1-m net catches for six representative euphausiid species. At small body lengths, ratios favor 1-m net, and at larger sizes ratios favor Bongo net, with maxima tending to fall at 13–19 mm and at >22-mm length.

Juvenile and Adult Avoidance

Toward the end of larval life, natatory function is transferred from antennae to pleopods, and antennae become sensory. These new capacities evidently better serve the animal in relation to the approach of the 1-m net than the Bongo. They increase rapidly in the postlarval period, 6-7 mm in *E. pacifica* and 6-8-mm in *N. difficilis*, followed by a diminished rate of increase through the juvenile phase. For the adult phase of most species, the rate of increase in the relative efficiency of the Bongo net is greatest.

The two *Stylocheiron* species (Figure 18B) seemed least affected by differences between the samplers.

The catches were nearly equal. The eye of these non-migrators consists of two differently oriented lobes, each with facets of a particular size. It may be rotated in the sagittal plane. *S. affine* and *S. longicorne* show strong daytime net-avoidance ability in their thermocline habitats (Brinton 1967a). They may have greater visual than tactile perception of predators, as may also be inferred in the present study from the equal abundances found by different nets during darkness. Land (1980) described function of the euphausiid bilobed eye in *Nematoscelis* in relation to daylight. He concluded that the upper lobe is designed to detect prey objects against downwelling light and the lower lobe to detect animals that reflect downwelled light against the dark background below.

On the other hand, vertically migrating round-eyed species such as comprise the genus *Euphausia*, live in near darkness day and night. They may therefore be relying more upon tactile than visual receptors in sensing the approach of predators, hence their better ability to better sense the bridled net than the 1-m net at night.

Sex Ratio, as Function of Net Type

Males of *Euphausia pacifica* outnumbered females in the Bongo samples by 1.1 to 1.0. This is construed to be a best estimate of the real sex ratio because both sexes are better sampled by the Bongo. The ratio in the 1-m net samples was 1.37:1, favoring females. A sex ratio for *E. pacifica* based on 1-m net samples from other years favored females, by 1.34:1 (Brinton 1976). The Bongo/1-m-net catch ratio was higher for males than females at all 1-mm body-length increments (Figure 10).

In *Nematoscelis difficilis*, males outnumbered females during early adulthood, 15-16 mm in Bongo samples, and 15-17 mm in 1-m net samples (Figure 12A). At greater body lengths, females outnumbered males, either due to higher mortality rates in males or to their better ability to avoid capture. An overall sex ratio favors females by 1.2:1 in the Bongo samples and by 1.1:1 in the 1-m net samples. The Bongo/1-m-net catch ratio was greater for males than for females at body lengths greater than 18 mm in this species. Thus, only these largest males of *N. difficilis* tend to avoid the 1-m net more effectively than females.

Bongo/1-m net Ratios of Abundance and Biomass

Much of the biogeographical mapping and study of euphausiid populations in the California Current has been based on CalCOFI surveys of 1950-76, during which the 1-m net was employed. The present data indicate that, for adult euphausiids at least, abundances estimated from the 1-m net catches are substantially less than those from the Bongo net. On the other hand, larvae, and in some species, juveniles, tend to be caught better by the 1-m net. Total numbers usually differed little between the two nets.

Ratios comparing Bongo and 1-m net catches of the principal life phases of the 12 euphausiid species are given in Table 1. These factors would not alter biogeographical information. An order of magnitude has commonly been used to separate intervals of total abundance (e.g. Brinton 1967b).

In the study of population dynamics, as in *Euphausia pacifica* (Brinton 1976), the larger number of juveniles and adults retained by the Bongo will significantly affect estimations of survivorship. They are already seen to clarify modes in length frequencies (e.g. Figures 5-7), the time progressions of which are used to determine growth rates. However, a danger in applying correction factors is that the factors cannot, as yet, deal with inconsistencies in catching capacity related to season or population structure. Furthermore, for large adults the factor would often be an unmanageable "infinity." Estimates of annual abundance or biomass of life phases (Table 1) rather than of 1-mm body-length increments, appear amenable to correction.

The Bongo/1-m net ratio for adult *Nematoscelis difficilis* is particularly high, 3.7, even in these nighttime samples. Strong daytime net avoidance by *N. megalops*, the Atlantic Ocean sibling of *N. difficilis*, led Wiebe and Boyd (1978) to question whether *N. megalops* engages in vertical migration at all. Adults of our two largest species, *Thysanoessa spinifera* and *Nematobrachion flexipes*, appear to be the strongest nighttime avoiders of the 1-m net, relative to the Bongo.

Biomass estimates are particularly affected by the Bongo/1-m net factors given in Table 1, because the bulk of biomass for the mean population of each species is seen to exist in juveniles and adults—for *E. pacifica*, 69% based on 1-m net sampling and 88% based on Bongo sampling, and in *Nematoscelis difficilis*, 91% and 96% respectively. For this reason, the mean biomass of the California population of *E. pacifica* is 1.7 times greater when measured by the Bongo than by the 1-m net, and of *N. difficilis*, 3.1 times greater.

Avoidance of the 1-m net has been described here only in relation to the Bongo-net catch. Bioluminescence and pressure signals are certain to be associated with any net and to prompt avoidance behavior by active plankters, as yet unmeasured in absolute terms.

ACKNOWLEDGMENTS

We are pleased to acknowledge the collaboration of

TABLE 1.
Bongo/1-m-Net Mean Catch Ratios of Abundance and Biomass

Species	Number of Stations	Abundance (Number/1000 m³)				Biomass (wet cc/1000 m³)			
		Larvae	Juveniles	Adults	Total	Larvae	Juveniles	Adults	Total
Euphausia pacifica	40	1864/2705 = 0.7	1028/792 = 1.3	379/149 = 2.5	3271/3646 = 0.9	2711/4111 = 0.7	9142/6034 = 1.5	10290/3223 = 3.2	22143/13368 = 1.7
E. eximia	27	51/63 = 0.8	25/26 = 1.0	6/3 = 2.0	82/92 = 0.9	33/39 = 0.8	174/198 = 0.9	446/184 = 2.4	653/421 = 1.5
E. gibboides	41	289/349 = 0.8	59/37 = 1.6	20/8 = 2.4	368/394 = 0.9	135/163 = 0.8	448/273 = 1.6	1423/723 = 2.0	2006/1159 = 1.7
E. recurva	27	61/65 = 0.9	28/28 = 1.0	45/28 = 1.6	133/120 = 1.1	31/34 = 0.9	65/64 = 1.0	555/319 = 1.7	651/417 = 1.6
E. hemigibba	17	5/5 = 1.0	15/8 = 1.7	14/8 = 1.7	34/21 = 1.6	2/2 = 1.0	28/12 = 2.3	172/95 = 1.8	202/109 = 1.9
Nyctiphanes simplex	23	260/649 = 0.4	298/1242 = 0.2	200/154 = 1.3	758/2045 = 0.4	142/418 = 0.3	739/2888 = 0.3	1958/946 = 2.1	2839/4252 = 0.7
Nematoscelis difficilis	56	368/479 = 0.8	220/132 = 1.7	118/32 = 3.7	706/643 = 1.1	184/246 = 0.7	1245/597 = 2.1	6580/1767 = 3.7	8009/2610 = 3.1
Thysanoessa gregaria	56	130/109 = 1.2	120/122 = 1.0	83/49 = 1.7	333/280 = 1.2	48/41 = 1.2	162/158 = 1.0	582/334 = 1.7	792/533 = 1.5
T. spinifera	17	323/734 = 0.4	112/46 = 2.4	3/0.1 = 30	438/780 = 0.6	629/718 = 0.9	1174/475 = 2.4	130/2 = 65	1933/1195 = 1.6
Nematobrachion flexipes	37	10/9 = 1.1	46/38 = 1.2	2/0.1 = 20	58/47 = 1.2	9/7 = 1.3	188/157 = 1.2	221/8 = 26.1	418/172 = 2.4
Stylocheiron affine	46	58/65 = 0.9	119/118 = 1.0	54/59 = 0.9	231/242 = 1.0	22/25 = 0.9	178/176 = 1.0	259/281 = 0.9	459/482 = 1.0
S. longicorne	46	16/18 = 0.9	29/26 = 1.1	17/18 = 0.9	62/62 = 1.0	7/7 = 1.0	40/35 = 1.1	102/108 = 0.9	149/150 = 1.0

the Instituto Nacional de Pesca of Mexico. Portions of these data were collected under authority of the Secretaria de Relaciones Exteriores and the Departamento de Pesca of Mexico.

This work was supported by the Marine Life Research Program, the Scripps Institution's component of the California Cooperative Oceanic Fisheries Investigations, and by the National Science Foundation, NSF Grant GA-26192.

LITERATURE CITED

Ahlstrom, E.H. 1952. Pilchard eggs and larvae and other fish larvae, Pacific Coast—1950. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 80, 8 p.

Aron, W. 1962. Some aspects of sampling the macroplankton. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 153:29–38.

Aron, W., and S. Collard. 1969. A study of the influence of net speed on catch. Limnol. Oceanogr. 14(2):242–249.

Brinton, E. 1962a. Variable factors affecting the apparent range and estimated concentration of euphausiids in the North Pacific. Pacif. Sci. 16(4):374–408.

———. 1962b. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr. 8(2):51–270.

———. 1967a. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12(3):451-483.

———. 1967b. Distributional atlas of Euphausiacea (Crustacea) in the California Current region, Part I, Calif. Coop. Oceanic Fish. Invest. Atlas 5, iii-xi, charts 1–275.

———. 1973. Distributional atlas of Euphausiacea (Crustacea) in the California Current region, Part II, Calif. Coop. Oceanic Fish. Invest. Atlas 18, v-vii, charts 1–336.

———. 1976. Population biology of *Euphausia pacifica* off southern California. Fish. Bull., U.S. 74(4):733–762.

———. 1979. Parameters relating to the distribution of planktonic organisms, especially euphausiids in the eastern tropical Pacific. Prog. Oceanogr. 8(3):125–189.

———. 1981. Effects of the warm winter/spring of 1977–78 on California Current euphausiid distribution in the context of 1953–63 events. Calif. Coop. Oceanic Fish. Invest. Rep. 22: (this volume).

Brinton, E., and J.G. Wyllie. 1976. Distributional atlas of euphausiid growth stages off southern California, 1953 through 1956. Calif. Coop. Oceanic Fish. Invest. Atlas 24, vii-xxxii, charts 1–289.

Clutter, R.I., and M. Anraku. 1968. Avoidance of samplers. *In* D.J. Tranter (ed.), Zooplankton sampling. UNESCO, p. 57–76.

Hansen, V.K. 1960. Investigations on the quantitative and qualitative distribution of zooplankton in the southern part of the Norwegian Sea. Meddr. Kommn Havunders., N.S. 2(23):1–53.

Land, M.F. 1980. Eye movements and the mechanism of vertical steering in euphausiid crustacea. J. Comp. Physiol. 137:255–265.

Longhurst, A.R., A.D. Reith, R.E. Bower, and D.L.R. Seibert. 1966. A new system for the collection of multiple serial plankton samples. Deep Sea Res. 13:213–222.

McGowan, J.A., and D.M. Brown. 1966. A new opening-closing paired zooplankton net. Univ. Calif. Scripps Inst. Oceanogr. Ref. 66–23.

McGowan, J.A., and V.J. Fraundorf. 1966. The relation between size of net used and estimates of zooplankton diversity. Limnol. Oceanogr. 11(4):456–469.

Mackintosh, N.A. 1934. Distribution of the macroplankton in the Atlantic sector of the Antarctic. Discovery Rep. 9:65–160.

Sands, N.J. 1978. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Comparison of the catch of the more numerous species by two different nets. Sarsia 63:237–246.

Tranter, D.J. 1966. Influence of net size and hauling velocity on zooplankton avoidance. Sym. Hydrodynamics of Plankton Samplers. ICES-SCOR-UNESCO WG on Zooplankton, 2247.

Wiebe, P.H., and S.H. Boyd. 1978. Limits of *Nematoscelis megalops* in the northwestern Atlantic in relation to Gulf Stream cold core rings. I. Horizontal and vertical distributions. J. Mar. Res. 36(1):119–142.