

## Distribution, Morphometry, and Seasonal Biology of the Planktonic Copepods *Neocalanus robustior* and *Neocalanus gracilis* in the Pacific Ocean<sup>1</sup>

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EXAMINATION of the comparative ecology of closely related species of oceanic, subtropical zooplankton may give some insight into the division of resources between potential competitors in an environment of relatively high physical stability and homogeneity, where finely divided, dispersed particulate matter constitutes the potential food for many species. The present study is similar to that of Mullin (1969) in that it discusses the geographical and vertical distributions, sizes of body and mouthparts, and breeding seasons of two congeneric, particle-grazing, calanoid copepods that are sympatric in tropical and subtropical waters. In the previous study, *Calanus tenuicornis* was found to have a broader geographical range than its larger congener, *C. lighti*, and to live in deeper water, at least during the autumn; no evidence was found for character displacement in size of mouthparts or for seasonal separation of reproduction in the Central North Pacific.

The present study concerns another pair of sibling species, *Neocalanus robustior* (Geisbrecht) and *N. gracilis* (Dana), that possess elongate first antennae and that differ from each other mainly in size. These species have often been placed in the genus *Calanus* (*sensu lato*) (e.g., recently, Bowman 1955, Brodsky 1967a) but are distinguished from other members of that genus by a strong, hooked spine on the anterior surface of the second basipodal segment of the

first pair of swimming legs. Bradford and Jillett (1974) have proposed that *Calanus cristatus*, *C. plumchrus*, and *C. tonsus* be included in the genus *Neocalanus*, although these species have relatively shorter antennae and lack the hook on the first pair of legs. The female *N. robustior* is distinguished from *N. gracilis* by the former's ventrally swollen genital segment and larger body size; in the males, the endopodite of the left fifth swimming leg of *N. robustior* is considerably reduced, while that of *N. gracilis* is only slightly so (cf. Brodsky 1967b), and *N. robustior* is again the larger. Copepodite stages of the two species may be distinguished by size (see below). Our specimens of both species have a dorsal projection at the posterior border of the head, but this character is more pronounced in *N. robustior*.

Both species have been reported from the Pacific (Grice 1962, and references therein), Atlantic (references in Vervoort 1946), and Indian (Sewell 1947, and references therein) oceans. They are among the 20 numerically most important species of large copepods in the Central Gyre of the North Pacific (Morris 1970; McGowan, personal communication).

### Zoogeographic Distribution in the Pacific

Plankton collections at the Scripps Institution of Oceanography were subsampled with a plankton splitter, and the copepodite stages III, IV, V, and VI (adults) of the two species were counted in aliquots. The samples were taken during the following expeditions: Shellback, May, June, and August 1952; Capricorn, December-February 1952-1953; Transpac, September-November 1953; Norpac, July-September 1955; Troll, March-April 1955; Equapac, August-September 1956; Downwind, October-February 1957-1958; Step I, November 1960; Tethys, June-August 1960;

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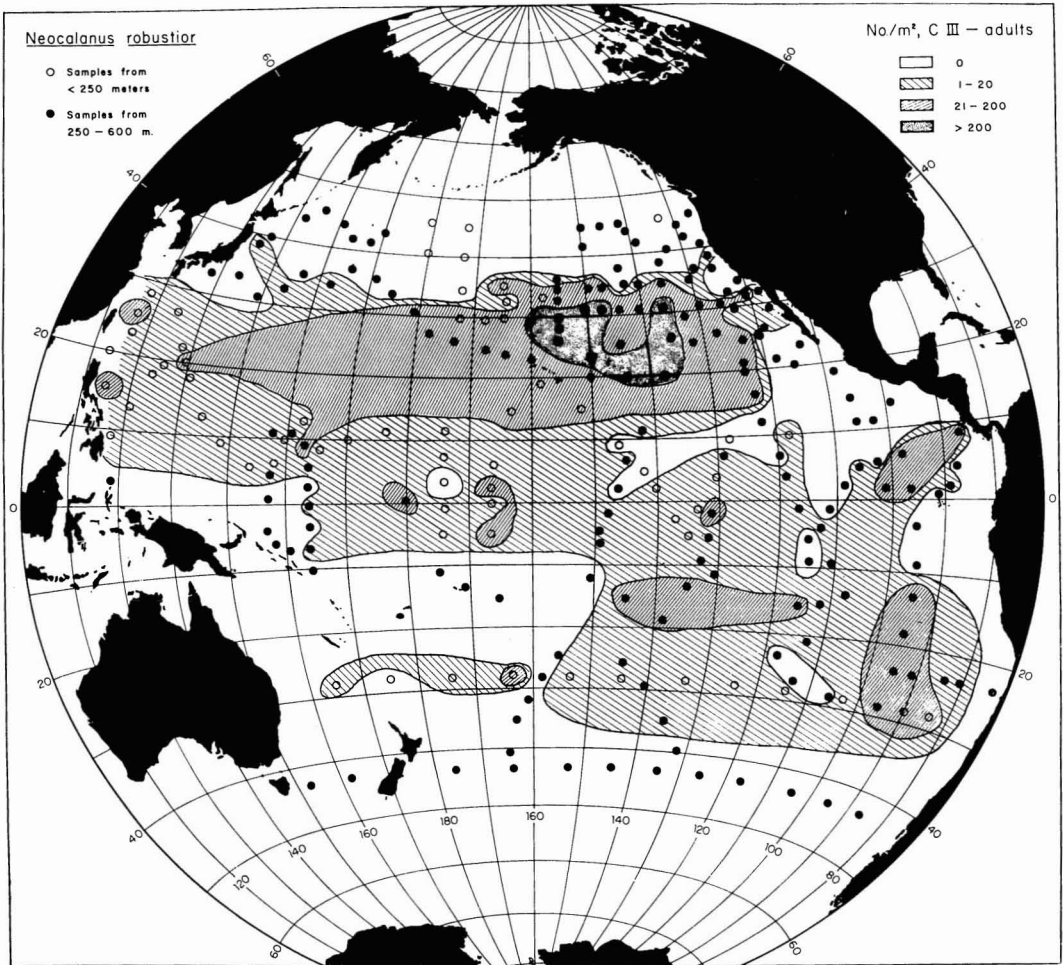


FIGURE 1. Distribution of *Neocalanus robustior* in the Pacific Ocean. Tows were taken from the surface to the depth indicated by open or filled circles. Contour intervals were chosen arbitrarily, based on breaks in the data on abundances.

Monsoon, March–April 1960–1961; Ursa Major, September 1964; Zetes, January 1966; and Scorpio, March–May 1967. Most of the samples were taken by oblique tows to various depths, generally with a net of 500–550  $\mu$  mesh netting and 1 m mouth diameter, with a flowmeter mounted in the mouth. All tows fished to at least 100 m, and tows which had fished to at least 250 m were used wherever possible so that the depths of maximal abundance of the species were reached (see later). Details concerning dates and locations of samples may be found in Snyder and Fleming (1965).

*Neocalanus robustior* is most abundant in the eastern Central North Pacific (Figure 1); it occurs only occasionally north of 35° N, and is rare or absent in the eastern tropical Pacific, the Peru–Chile Current, and the western South Pacific. The distribution of *N. gracilis* (Figure 2) is similar, both species being warm-water cosmopolites in the terminology of McGowan (1971), but the range of *N. gracilis* extends farther to the north (see also Park 1968, table 2) and south, and this species is relatively more common in the western South Pacific than is *N. robustior*. It should be noted, however, that

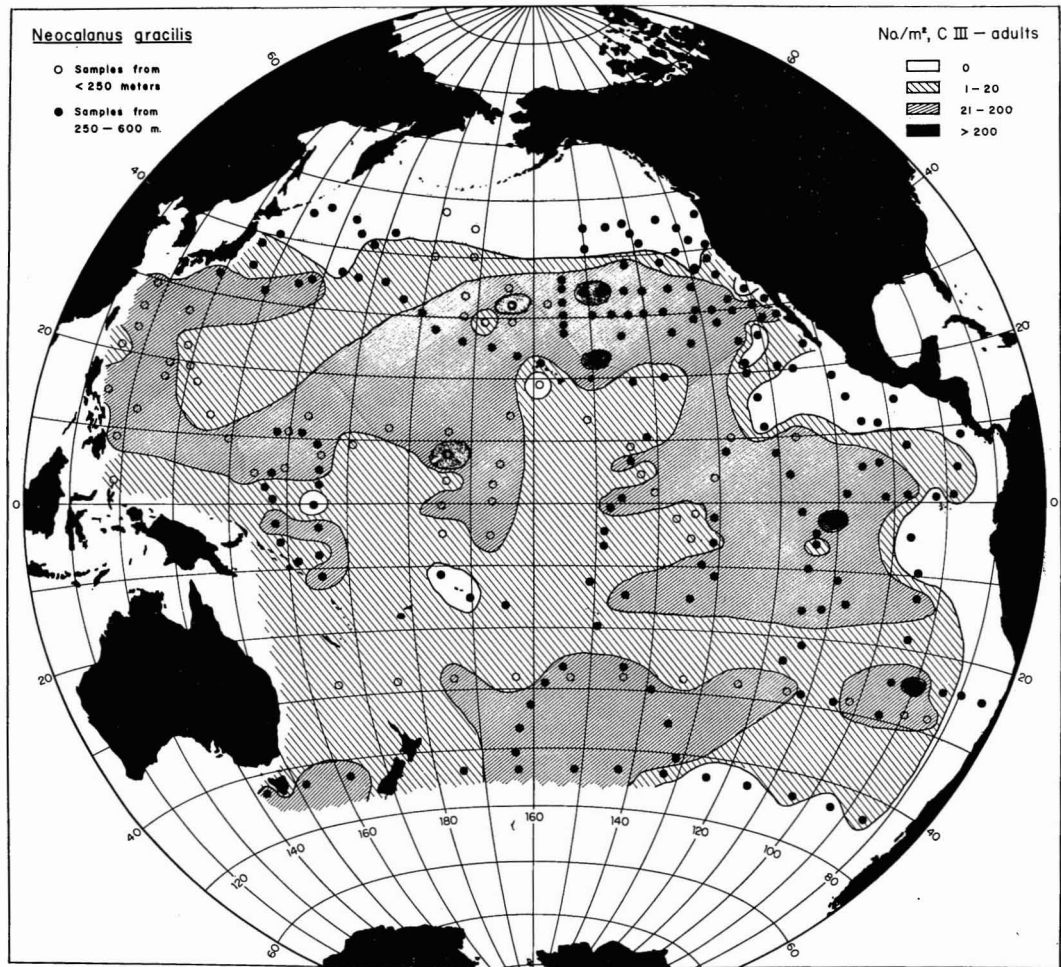


FIGURE 2. Distribution of *Neocalanus gracilis* in the Pacific Ocean. Tows were taken from the surface to the depth indicated by open or filled circles. Contour intervals were chosen arbitrarily and were based on breaks in the data on abundances.

Morris (1970) reported both species as far north as 44° N in a transect along 160° W (not 160° E as reported in the title). Heinrich (1969) reported that both species were much less abundant in the western South Pacific than in the western North Pacific.

These conclusions may be biased, of course, by the season or year in which each area was sampled, if the species have pronounced seasonal cycles or year-to-year changes in abundance. Data concerning the abundances of the two species in the eastern Central North Pacific in various months are given below.

#### Morphometry

As discussed previously (Mullin 1969, and references cited therein), the differences in body size of sympatric congeners could indicate differences between the species in selection of sizes of particles of food, or could facilitate reproductive isolation of the species, or both. Therefore, cephalothoracic (= prosomal) lengths of at least 10 individuals of each developmental stage of *Neocalanus* were measured by means of an ocular micrometer, the animals having been taken from stations representing particular zoogeographical areas. Since sizes

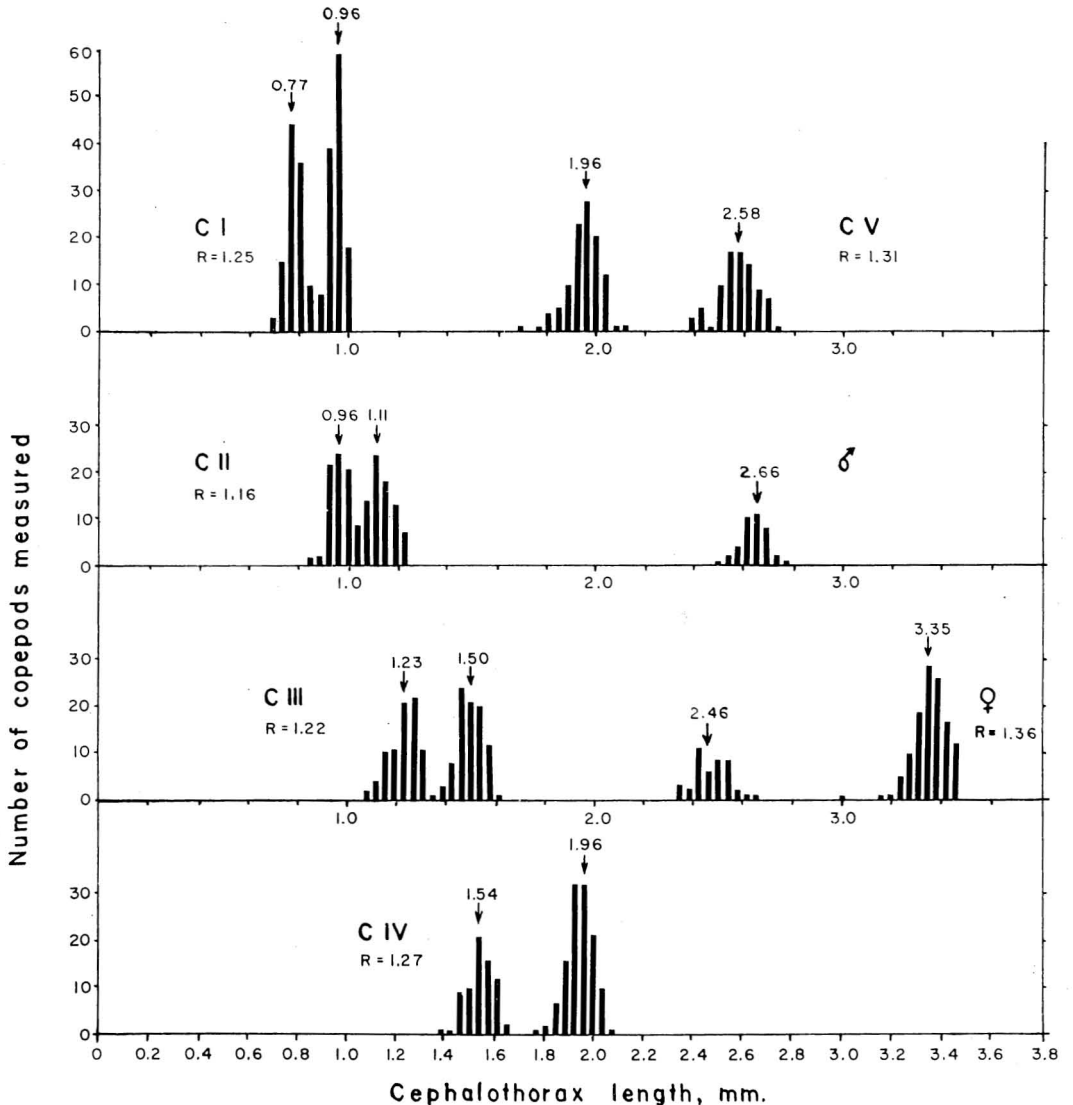


FIGURE 3. Sizes of copepodite stages of *Neocalanus gracilis* and *N. robustior* from 28° N, 155° W in August 1969. For each stage, the arrows and numbers above the histograms indicate the median cephalothorax (prosomal) length of the individuals assigned to each species, *N. gracilis* being the smaller in each case. The value of R is the ratio of median lengths of the two species at that stage. No male *N. gracilis* was found at this particular station; males of this species from other stations had a median cephalothorax length of 2.12 mm, with a range from 1.94 to 2.31 mm, which would result in  $R = 1.25$  for males.

of mouthparts might be more directly related to the sizes of food particles which can be ingested, a mandibular blade (gnathobase) was removed from each animal and pressed flat under a cover slip on a glass slide, and the width of its molariform edge was measured by means of an ocular micrometer.

Figure 3 shows the sizes of all copepodite stages of both species taken from a single station in the Central North Pacific. Copepodites of the two species may be clearly distinguished by size at stage III. The size distributions of earlier stages, although overlapping, are obviously bimodal and permit most individuals to

be assigned to one species or the other with reasonable certainty. Although the median size of any particular stage varies somewhat between stations and seasons, the bimodality always (in our experience) permits separation of the species in all copepodite stages. It is interesting that the size of any one copepodite stage of *N. robustior* is in most cases very close to the size of the next older stage of *N. gracilis*, prior to adulthood.

Hutchinson (1959) suggested that a ratio of at least 1.3:1 in the sizes of food-gathering structures of congeneric species permitted coexistence in separate trophic niches. The ratio of cephalothoracic lengths of the two species at any one stage exceeds 1.3 only in the copepodite stage Vs and adult females. As in the sibling pair *Calanus lighti* and *C. tenuicornis* (Mullin 1969), the widths of the mandibular blades are more similar between the two species of *Neocalanus* in any developmental stage than are the cephalothoracic lengths; the smaller *N. gracilis* in the Central North Pacific has a mandibular width:cephalothoracic length ratio of 0.072–0.073 (median values for 26 females and 27 copepodite Vs), while the larger *N. robustior* has a ratio of 0.068–0.069 (medians for 28 females and 26 copepodite Vs). Hence, even for adult females, the ratio of mandibular widths of the two species is slightly less than 1.3:1. If the two species of *Neocalanus* have been under competitive pressure to diverge in the sizes of food particles they are capable of ingesting, this pressure is not reflected as character displacement in size of the mandibular blades.

For each species, the mandibular:cephalothoracic ratios of the copepodite stages II, III, and IV were very similar to the ratios found for copepodite stage V and for female individuals of the same species. In the first copepodite stage (copepodite I) of each species, the ratio is considerably less because the outermost cusp of the mandibular blade has not yet developed.

A small number of measurements (Table 1) indicate that *N. robustior* is smaller in body size in the Central South Pacific than in the North Pacific ( $P < 0.01$  by rank sum test that the medians are the same as those given in Figure 3). This is not true for *N. gracilis*, so the difference in size between the species is less in

the Central South Pacific than in the North Pacific. In the northern part of the North Pacific where it occurs allopatrically, *N. gracilis* is larger in body size, and is still larger in its area of allopatry in the southern South Pacific (Table 1). This situation superficially resembles that found in *Calanus lighti* and *C. tenuicornis*, in that the body size of the smaller species (*C. tenuicornis* and *N. gracilis*) increases in areas of cooler surface water where its larger congener does not occur. Indeed, the lower mandibular:cephalothoracic ratio of the *N. gracilis* from 40°–43° S parallels the trend shown by the “intermediate form” of *Calanus tenuicornis* (Mullin 1969), a geographic isolate in the southern South Pacific that shows apparent morphometric convergence toward the larger *C. lighti*. In the case of *Neocalanus gracilis*, however, the mandibular:cephalothoracic ratio in the southern South Pacific does not distinguish it from the populations in other regions since this ratio decreases with increasing cephalothoracic length throughout the range of the species (Table 1). (The hypothesis that a common regression line for all populations adequately describes the relationship of mandibular width to cephalothoracic length was acceptable;  $P \gg 0.10$ .)

#### *Seasonality in the Eastern Central North Pacific*

In temperate waters, congeneric species often occur or at least have maximal abundances in different seasons, so that a temporal separation of niches results. In subtropical oceans, where seasonal variation in physical parameters is less extreme, temporal separation of niches might be less important. In order to examine this question, we counted animals of copepodite stage IV and older that had been caught in net tows taken from the surface to at least 250 m in the area 125°–160° W, 20°–35° N, and plotted the counts with respect to date, irrespective of year (Figure 4). Some individuals, especially *N. gracilis*, may occur deeper than the maximum depth of some of the tows, but any seasonal cycle of abundance should be reflected inasmuch as the bulk of the population was sampled, and inasmuch as the copepodite stages counted should have been retained quantitatively by the meshes of the different nets used.

TABLE 1  
 CEPHALOTHORACIC LENGTH AND MANDIBULAR WIDTH: CEPHALOTHORACIC LENGTH, BY AREA,  
 OF *Neocalanus robustior* AND *N. gracilis*

| AREA                       | CEPHALOTHORACIC LENGTH (mm) |      |                            |      | MANDIBULAR WIDTH:<br>CEPHALOTHORACIC LENGTH |       |                            |       |
|----------------------------|-----------------------------|------|----------------------------|------|---|-------|----------------------------|-------|
|                            | <i>Neocalanus robustior</i> |      | <i>Neocalanus gracilis</i> |      | <i>Neocalanus robustior</i>                 |       | <i>Neocalanus gracilis</i> |       |
|                            | COPEPODID                   |      | COPEPODID                  |      | COPEPODID                                   |       | COPEPODID                  |       |
|                            | FEMALE                      | V    | FEMALE                     | V    | FEMALE                                      | V     | FEMALE                     | V     |
| 12°- 16° S,<br>112°-135° W |                             |      |                            |      |   |       |                            |       |
| Median                     | 3.21                        | 2.48 | 2.50                       | 2.00 | 0.069                                       | 0.069 | 0.075                      | 0.072 |
| N                          | 13                          | 18   | 29                         | 20   |   |       |                            |       |
| 34°- 39° N,<br>125°-173° W |                             |      |                            |      |   |       |                            |       |
| Median                     | *                           | *    | 2.81                       | 2.24 | *   | *     | 0.069                      | 0.067 |
| N                          | *                           | *    | 12                         | 15   | *   | *     |                            |       |
| 40°- 43° S,<br>132°-165° W |                             |      |                            |      |   |       |                            |       |
| Median                     | *                           | *    | 3.26                       | 2.53 | *   | *     | 0.064                      | 0.064 |
| N                          | *                           | *    | 24                         | 22   | *   | *     |                            |       |

NOTE: 2-4 stations were pooled in each zoogeographic area. Compare with Figure 3 and text concerning specimens from the Central North Pacific.

\* No occurrences in samples examined.

The samples from the eastern Central North Pacific that were used to prepare Figures 1 and 2 were taken in August; Figure 4 (which includes data from these samples) supports the impression that *N. robustior* is the more abundant species in the fall and winter. Even during these seasons, however, *N. gracilis* is the more common in a few samples. The population of *N. gracilis* may reach its maximum somewhat earlier in the year than does that of *N. robustior*, but too few years were sampled in the same seasons to allow us to determine if this is a recurring pattern. Deevey (1971) reported that *N. gracilis* occurs year-round off Bermuda but in insufficient numbers for description of a seasonal cycle.

The median abundances for all samples were 88 *N. robustior* and 40 *N. gracilis* per m<sup>2</sup>; these medians partly reflect the uneven distribution of samples throughout the year. Since year-to-year and location-to-location variability is suppressed in Figure 4, all of the 111 pairs of values for abundances of the two species were plotted as a scatter diagram and examined for degree of association by a corner test (Tate and

Clelland 1957: 67-69). If the species tend to be abundant in different seasons, years, or even locations, then a negative correlation might exist between their abundances; in fact, the correlation is significantly positive ( $P = 0.05$ ). This statistical test is particularly sensitive to extremes, i.e., very high or very low abundances. Therefore the observed correlation could either be real (both species are abundant or rare at the same times and places) or spurious (e.g., if the volume of water filtered by a particular tow was grossly over- or underestimated, the apparent abundances of both species will be spuriously low or high). At the very least, however, this result is inconsistent with spatial or temporal distinctness of the two species within the eastern Central North Pacific.

Even though the late copepodite stages do not appear to be separated in the Central North Pacific either areally or temporarily, the species might be long-lived and breed in different seasons so that the younger developmental stages would occur at different times. Males of both species have reduced mandibular blades and, because of starvation, probably do not



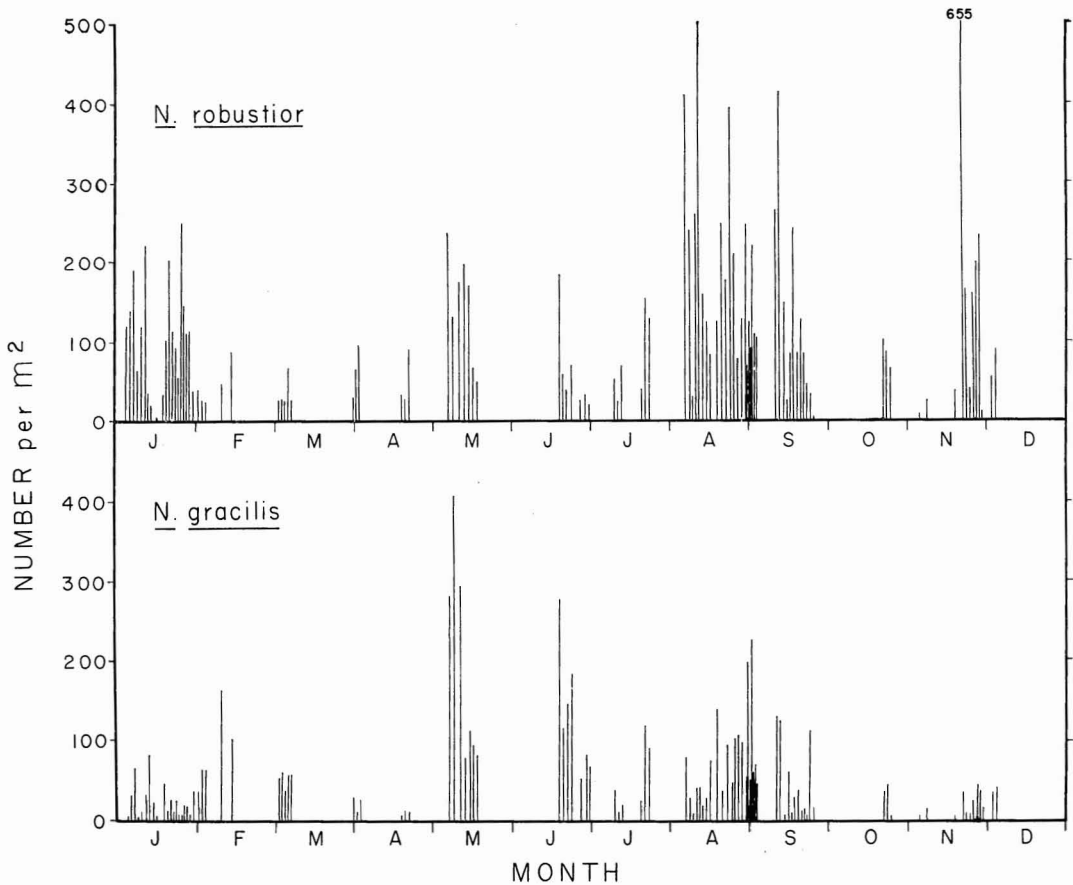


FIGURE 4. Abundances of *Neocalanus robustior* and *N. gracilis*, copepodite IV to adult, in the eastern Central North Pacific.

survive adulthood nearly as long as do the females. Hence, a distinct breeding season should be detectable as an increase in the ratio of males to females. Figure 5 shows the mean sex ratio for each half-month period in the eastern Central North Pacific; although there is considerable variation, there is no clearly defined seasonality. The median ratios of males to females are 0.17 and 0.14 for *N. robustior* and *N. gracilis*, respectively. A corner test on the sex ratios in all samples indicated no correlation between the ratios. Thus, there is no evidence that the breeding activities of the two species are separate in location or time.

#### Vertical Distribution

Both species are known to occur predominantly in the upper few hundred meters, but findings have differed as to the precise vertical distributions of the two species. Vervoort (1946) reported *N. gracilis* to be found from the surface to 1000 m, being most common at middepths, and that it does not undertake a diurnal vertical migration. *N. robustior* was found mainly near the surface, and Vervoort disagreed with an earlier report (Rose 1933) of diurnal vertical migration in this species. Vinogradov (1968) reported that *N. gracilis* was most abundant in the upper 200 m in the equatorial Pacific, but that the vertical range extends to 500–1000 m in the Pacific and even deeper in the Mediterranean. *N. robustior* also

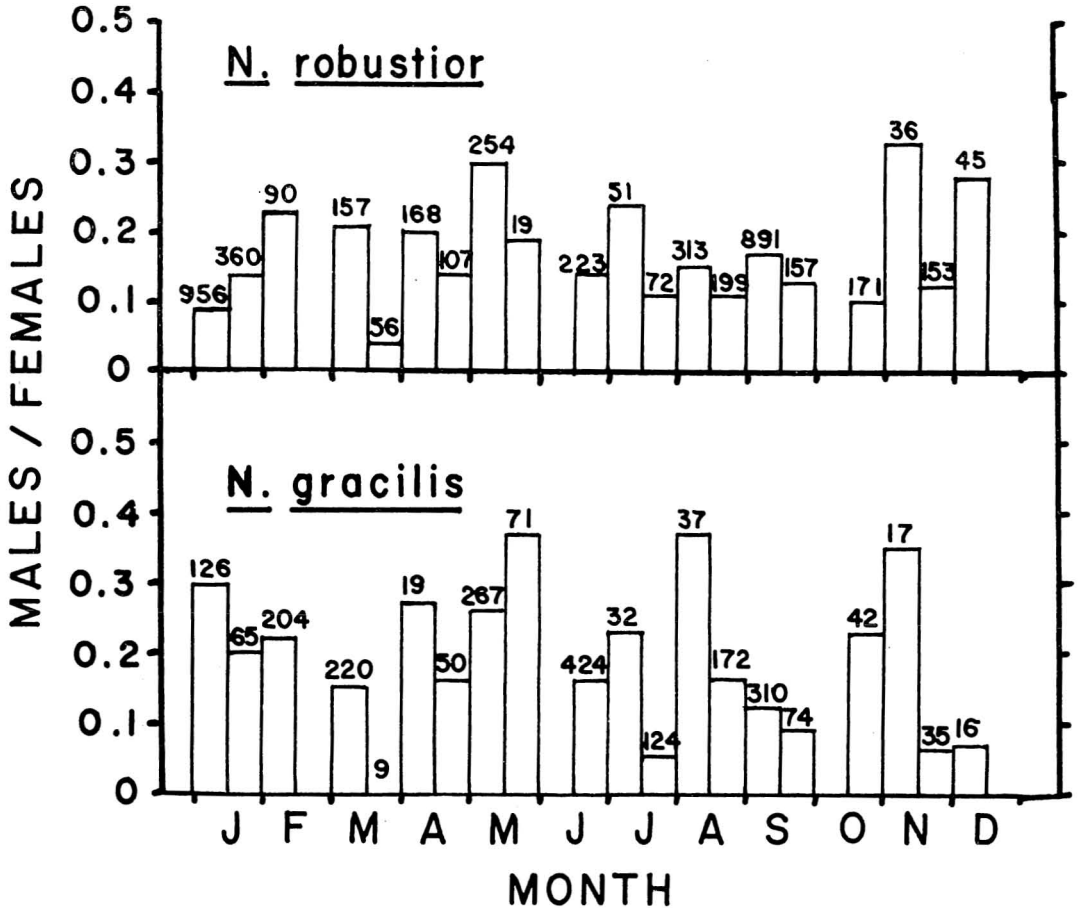


FIGURE 5. Sex ratios of *Neocalanus robustior* and *N. gracilis* in the eastern Central North Pacific. The number above each bar indicates the total number of adults counted; absence of bar and number indicates that no samples were taken in that half-month.

apparently occurs deeper in the Mediterranean than in other seas. The *N. gracilis* populations in the Pacific Central Water Masses have been reported to migrate from approximately 300 m in the daytime to approximately 50 m at night (Vinogradov 1968), the migration being over a shorter distance in equatorial waters. Grice and Hulsemann (1965) found both species occurring to a depth of 1000 m in the Atlantic. However, Roe (1972a) found *N. robustior* only in the upper 250 m day and night at a tropical Atlantic station; he found *N. gracilis* to 1000 m and believed it to have a weakly developed diurnal vertical migration.

Vertical distributions of the two species reported here are based on catches of opening-

closing bongo nets (McGowan and Brown 1966). Samples were taken on two transects along 155° W from Hawaii into the Alaska Gyre (cruises Zetes, January 1960; and Ursa Major, September 1964) with 505  $\mu$  mesh nets, and at single stations sampled both day and night with 183  $\mu$  mesh nets on the following cruises: Climax II, September 1969; FCRG 71-2, November 1971; Cato I, June 1972; C'Bog I, August 1972; Southtow XIII, February 1973; Tasaday I, June 1973, Tasaday XI, March 1974; and Dramamine II, May 1974. In all cases, subsamples equivalent to at least 10 m<sup>3</sup> of water filtered were counted. Only on Tasaday I were samples taken below 500 m.



Table 2 summarizes results from Southtow XIII, Tasaday I, and Dramamine II; data from other cruises are omitted for brevity but may be obtained from the senior author upon request. On all cruises, copepodite stages other than copepodite I and the males of *N. gracilis* were almost always found in greatest concentrations in the upper 100 m. *Neocalanus robustior* was essentially restricted to this vertical range on several occasions, while *N. gracilis* usually occurred below 100 m as well as above this depth. Both species could sometimes be found as deep as 850 m, as shown by the deep tows taken on Tasaday I (Table 2). The first copepodite stages of both species usually were most abundant at greater depths than were the older stages, possibly due to sinking of eggs prior to hatching and failure of the nauplii to return to the surface waters. This ontogenetic difference in vertical distribution was found for *N. gracilis* in the Adriatic Sea by Shmeleva and Zaika (1973). The greatest abundance of *N. gracilis* was usually found at a greater depth than that of *N. robustior* during the day, but this was not the case at night. At least part of the *N. gracilis* population appeared to migrate vertically, since individuals were captured in the most shallow tows at only 2 of 13 daytime stations but at all 11 stations sampled at night. Some copepodites of *N. robustior* were found in the most shallow tows at 11 of the 13 daytime stations, contrary to the impression given by Table 2.

The general impression created by all collections is that although the vertical distributions of the two species overlap considerably, the center of distribution of *N. gracilis* is somewhat deeper than that of *N. robustior* during the day. This is not unexpected, since the zoogeographic range of the former species extends into colder water than does that of the latter (Figures 1 and 2), and there is at least an analogy to the horizontal and vertical distributions of *Calanus tenuicornis* and *C. lighti* (Mullin 1969). At night, the depths of greatest abundance of the two species are much more likely to coincide, although the vertical range of *N. gracilis* is usually the greater.

#### DISCUSSION

Almost by definition, sympatric species occupy different ecological niches; of less certainty is the proposition that they must do so to avoid competitive exclusion and extinction of either. The latter statement may not be "proven" simply by the observation that ecological differences can usually be found between sympatric species, since the conclusion that these differences are sufficient to reduce competition to an acceptable level is invalid unless the extent and nature of the presumed competition have been demonstrated.

The pelagic environment seems to be relatively monotonous with respect to conventionally measured properties, although it may be rather more diverse from the zooplankter's point of view. In any case, the plants are all very small (with the obvious exception of *Sargassum*). This means that there is no physical cover or refuge for a prey species and that, in contrast to terrestrial environments where an individual plant may serve as both food and substratum for many herbivorous insects during much of their lives, the planktonic herbivores generally have no persistent spatial association with a particular species of food but must feed by filtration on a variety of particles.

In the two species of *Neocalanus*, as in *Calanus lighti* and *C. tenuicornis* (Mullin 1969), the sizes of the mandibular blades of any developmental stage are more similar than the sizes of the bodies. If there had been strong evolutionary pressure for divergence in size of feeding appendages between sympatric competitors, one would expect the mandibular blades to be at least as dissimilar as the bodies, or more so. In fact, failure to diverge could mean that the congeners do not compete for a common, limiting source of food; that divergence in selection of food is based on some property of the food particles other than their size or on a morphological feature other than mandibular width; or it could simply be a consequence of continuous breeding and the considerable increase in bodily size which accompanies juvenile development. Continuous breeding means that all developmental stages of both congeners are present in the water at any time. Hence, a slight increase in mandibular size of the larger

TABLE 2

VERTICAL DISTRIBUTIONS OF COPEPODID STAGES OF *Neocalanus robustior* AND *N. gracilis* AT APPROXIMATELY 28° N, 155° W

| CRUISE AND<br>DATE                     | TIME  | DEPTH<br>m                       | <i>Neocalanus robustior</i> |      |     |     |      |        |      | <i>Neocalanus gracilis</i> |      |      |     |      |        |      |     |   |
|--|-------|----------------------------------|-----------------------------|------|-----|-----|------|--------|------|----------------------------|------|------|-----|------|--------|------|-----|---|
|  |       |                                  | I                           | II   | III | IV  | V    | FEMALE | MALE | I                          | II   | III  | IV  | V    | FEMALE | MALE |     |   |
| Southtow<br>XIII, 5-6<br>February 1973 | 0904- | 25                               | *                           | 0.2  | 0.2 | 0.1 | 0.5  | 1.1    | *    | *                          | 0.1  | *    | *   | *    | *      | *    |     |   |
|  |       | 1045                             | 50                          | 0.1  | 0.3 | 0.4 | 0.2  | 0.3    | 0.6  | *                          | *    | 0.2  | 0.6 | 0.1  | 0.2    | *    | *   |   |
|  |       | 100                              | *                           | 0.3  | 0.3 | 0.7 | 2.0  | 1.1    | 0.2  | *                          | 0.7  | 2.0  | 1.1 | 3.3  | 3.2    | 0.4  |     |   |
|  |       | 200                              | *                           | *    | *   | *   | *    | *      | *    | 0.4                        | 0.3  | *    | *   | 0.2  | 0.1    | 0.1  |     |   |
|  |       | 300                              | *                           | *    | *   | *   | *    | *      | *    | 0.1                        | *    | *    | *   | *    | 0.1    | 0.1  |     |   |
|  | 2045- | 400                              | *                           | *    | *   | *   | *    | *      | *    | *                          | *    | *    | *   | 0.1  | *      | 0.1  |     |   |
|  |       | 25                               | *                           | 0.6  | 1.3 | 1.6 | 0.5  | 0.1    | *    | *                          | 0.2  | 2.4  | 2.9 | 1.9  | 1.4    | 0.2  |     |   |
|  |       | 0100                             | 50                          | *    | 0.6 | 2.2 | 1.9  | 4.5    | 1.5  | 0.3                        | *    | 0.2  | 0.7 | 0.5  | 0.3    | 0.6  | *   |   |
|  |       | 100                              | *                           | 0.9  | 2.7 | 1.1 | 3.7  | 0.7    | 0.2  | *                          | 0.9  | 2.7  | 5.5 | 0.5  | 5.9    | 0.5  |     |   |
|  |       | 200                              | 0.3                         | 0.2  | 0.3 | 0.3 | 1.1  | 0.3    | 0.1  | 0.3                        | 0.9  | 0.4  | 0.9 | 1.1  | 1.3    | 0.1  |     |   |
|  |       | 300                              | *                           | *    | *   | *   | *    | *      | *    | 0.1                        | *    | *    | *   | *    | 0.1    | *    |     |   |
|  |       | 400                              | *                           | *    | *   | *   | *    | *      | *    | *                          | *    | *    | *   | *    | 0.2    | 0.2  |     |   |
|  |       | Tasaday I,<br>19-21 June<br>1973 | 0937-                       | 20   | *   | *   | *    | *      | *    | *                          | *    | *    | *   | *    | *      | *    | *   | * |
|  |       |                                  |                             | 1130 | 50  | *   | 1.1  | 5.6    | 1.1  | 1.6                        | 15.8 | 0.9  | *   | *    | 0.7    | 0.7  | *   | * |
| 100                                    | *     |                                  |                             | 1.4  | *   | *   | *    | *      | *    | *                          | *    | 21.0 | 1.9 | 2.1  | 1.2    | *    | 0.1 |   |
| 200                                    | 1.3   |                                  |                             | 0.4  | *   | *   | *    | *      | *    | *                          | 4.4  | 0.7  | *   | *    | 0.1    | *    | *   |   |
| 300                                    | 1.1   |                                  |                             | *    | *   | *   | *    | *      | *    | *                          | 2.7  | 0.3  | *   | *    | 0.1    | *    | 0.2 |   |
| 2235-                                  | 400   |                                  | 1.1                         | *    | *   | *   | *    | *      | *    | *                          | 5.8  | 0.1  | *   | *    | *      | *    | 0.1 |   |
|  | 20    |                                  | *                           | *    | *   | *   | 2.4  | 1.1    | *    | *                          | *    | *    | 2.0 | 0.9  | 2.2    | *    |     |   |
|  | 0115  |                                  | 60                          | 0.2  | 5.8 | 2.2 | 0.4  | *      | 1.1  | *                          | 0.4  | 2.7  | 4.4 | *    | 1.6    | 0.7  | *   |   |
|  | 130   |                                  | 0.5                         | 1.8  | 0.2 | *   | *    | *      | *    | 0.2                        | 3.9  | 3.0  | *   | 0.9  | *      | 0.2  |     |   |
|  | 200   |                                  | 3.0                         | 0.3  | *   | *   | *    | *      | 0.2  | *                          | 3.2  | 0.1  | *   | *    | 0.2    | 0.3  |     |   |
| Dramamine<br>II, 11-12<br>May 1974     | 1020- | 240                              | 0.6                         | *    | *   | *   | *    | *      | *    | 1.8                        | 0.1  | *    | *   | *    | *      | 0.1  |     |   |
|  |       | 380                              | 2.5                         | *    | *   | *   | *    | *      | *    | 1.9                        | 0.1  | *    | *   | *    | *      | 0.1  |     |   |
|  |       | 700                              | 0.02                        | *    | *   | *   | 0.04 | *      | *    | 1.13                       | 0.02 | *    | *   | *    | 0.18   | 0.04 |     |   |
|  |       | 850                              | *                           | *    | *   | *   | 0.02 | *      | *    | *                          | *    | *    | *   | *    | 0.03   | *    |     |   |
|  |       | 10                               | *                           | *    | *   | *   | *    | *      | *    | *                          | *    | *    | *   | *    | *      | *    |     |   |
|  |       | 1330                             | 80                          | *    | 1.8 | 2.1 | 0.7  | 0.2    | 0.4  | 0.1                        | *    | *    | *   | 0.1  | *      | 0.1  | 0.1 |   |
|  |       | 150                              | 1.7                         | 0.1  | *   | *   | *    | *      | *    | *                          | 1.0  | *    | *   | *    | *      | *    | *   |   |
| 2135-                                  | 240   | 1.0                              | *                           | *    | *   | *   | *    | *      | *    | 1.5                        | *    | *    | *   | 0.1  | 0.2    | 0.3  |     |   |
|  | 360   | 1.2                              | *                           | *    | *   | *   | *    | *      | *    | 1.8                        | *    | *    | *   | *    | 0.1    | 0.1  |     |   |
|  | 490   | *                                | *                           | *    | *   | *   | *    | *      | *    | *                          | *    | *    | *   | *    | *      | 0.1  |     |   |
|  | 10    | *                                | *                           | 0.3  | 0.6 | 0.6 | 1.7  | 0.6    | *    | *                          | *    | *    | *   | 0.9  | *      |      |     |   |
|  | 0100  | 55                               | *                           | 0.2  | 4.7 | 4.9 | 2.0  | 0.4    | 1.1  | *                          | *    | 2.0  | 3.6 | 17.8 | 10.9   | 0.2  |     |   |
|  | 120   | *                                | *                           | *    | 1.1 | *   | 0.4  | 0.1    | 0.1  | *                          | *    | *    | *   | 0.1  | 0.1    |      |     |   |
|  | 210   | 0.2                              | *                           | *    | *   | *   | 0.2  | *      | 0.6  | *                          | *    | *    | *   | 1.1  | 0.6    | *    |     |   |
| 320                                    | 0.3   | *                                | *                           | *    | *   | *   | *    | 0.7    | *    | *                          | *    | *    | 0.6 | 0.1  |        |      |     |   |
| 430                                    | *     | *                                | *                           | 0.1  | *   | *   | *    | *      | *    | *                          | *    | *    | *   | *    | 0.1    |      |     |   |

NOTE: Values represent numbers of individuals per 10 m<sup>3</sup>.

congener may make it more distinct from the smaller at the same developmental stage, but at each stage except that of the adult female the mandibular size of the larger congener would still be very similar to the next older stage of the smaller congener. Similarly, little advantage may be gained by a reduction in mandibular size of the smaller of two congeners as long as the juvenile stages of the larger are always present.

Vertical partitioning of the pelagic habitat has often been cited as a means by which related species can reduce competition. Baker (1970) found that congeneric species of nonmigrating euphausiids tend to live at different depths, although migrating species overlap considerably in vertical distribution; Brinton's (1967) data do not indicate marked separation between congeneric euphausiids. Pugh (1974) found little vertical overlap in the ranges of 12 of 13 species of the nonmigrating siphonophore genus *Lensia*. Foxton (1970) felt that the daytime depths of congeneric decapods are reasonably distinct, and Clarke (1973) discussed the importance of different vertical distributions at night for morphologically similar myctophid fishes. Zalkina (1970) found that the centers of vertical distribution in the upper 300 m of tropical, cyclopoid copepods were different, and partial vertical separation of congeneric species of *Metridia* and *Pleuromamma* (calanoid copepods) is suggested by data of Roe (1972b).

The depths of maximal abundance of *Calanus lighti* and *C. tenuicornis* in the eastern Central North Pacific are distinct during at least part of the year. As in the present case, the species of smaller bodily size and greater geographical range tends to occur deeper in the water column. In both *Calanus* and *Neocalanus*, however, the overlap between congeners is considerable, and the efficacy or even the necessity of partial vertical separation as a means of reducing what would otherwise be intolerable competition remains to be demonstrated.

#### SUMMARY

1. *Neocalanus robustior* and *N. gracilis* are sympatric in much of the Pacific; the latter has a wider geographical range to the north and south. Both species are most abundant in

the upper 200 m in the eastern Central North Pacific; the center of distribution of *N. gracilis* is generally deeper than is that of *N. robustior* during the day.

2. The copepodite stages of the two species are distinguishable by body size, a given stage of *N. robustior* being approximately the size of the next older stage of *N. gracilis*. There was no evidence of character displacement in size of the mandibular blade.
3. Both species probably breed throughout the year in the eastern Central North Pacific, and there was no evidence that the seasonal patterns of abundance of the two species differ.

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