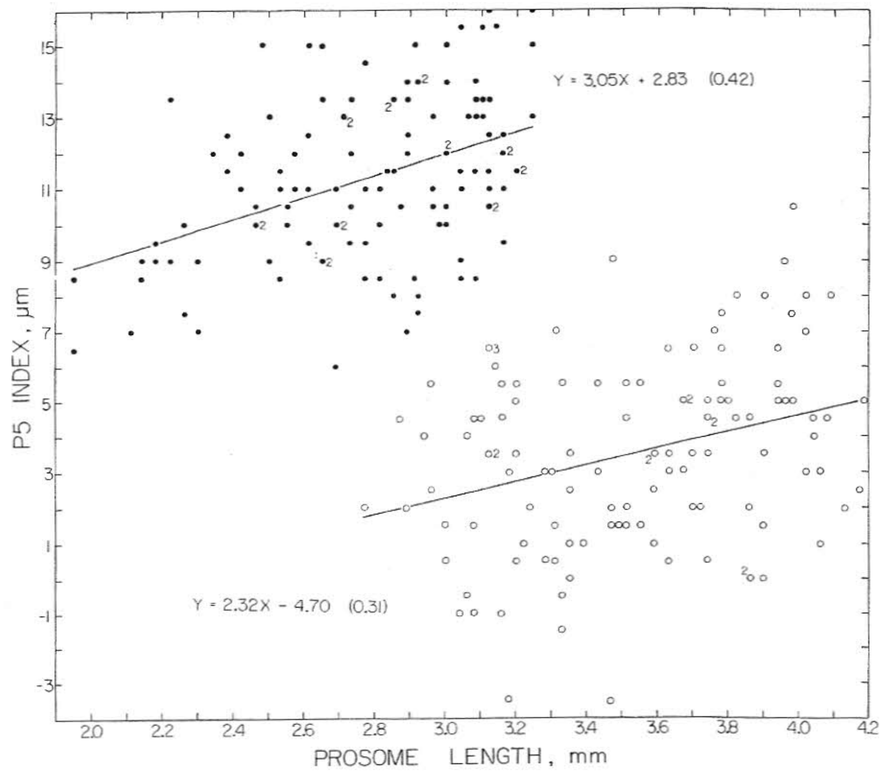

Fig. 9. *Calanus*. P5 Index (see p.8 plotted against prosome length (symbols as in Fig. 8). Data for Series A and B are combined. Slop of the two regression lines diffe significantly from zero ($P<0.001$ for both). Virtually entire range of length of each species is represented

Table 2. *Calanus finmarchicus* and *C. glacialis*. Range and variation of prosome length (mm) of adult females from two regions of allopatry (western North Atlantic Ocean and Central Arctic Ocean) a three regions of sympatry. Specimens were randomly selected from plankton samples collected a following location and dates: western North Atlantic Ocean (53°10'N; 45°31'W, April, 1964), G of Maine (44°25'N; 67°50'W, February, 1969), Greenland Sea (8 stations between 67°12'N; 25°34' and 77°01'N; 11°05'W, March-May, 1965), Barents Sea (78°40'N; 72°22'E, August, 1967), and cen Arctic Ocean (85°08'N; 88°50'W, May, 1971). r: range of length measurements; m: mean length o specimens; cv: coefficient of variation of length measurements; n: number of specimens measur

Region	Western North Atlantic	Gulf of Maine	Greenland Sea	Barents Sea	Central Arctic Ocean
			C. finmarchicus		
r	2.38-3.28	2.26-3.12	2.34-3.24	2.24-3.20	
m	2.84	2.69	2.84	2.71	
cv	6.75	7.94	5.49	7.45	
n	123	34	352	60	
			C. glacialis		
r		3.04-3.78	2.89-4.25	2.87-4.13	3.16-4.25
m		3.47	3.55	3.61	3.80
cv		5.87	6.86	7.69	5.33
n		26	484	123	169

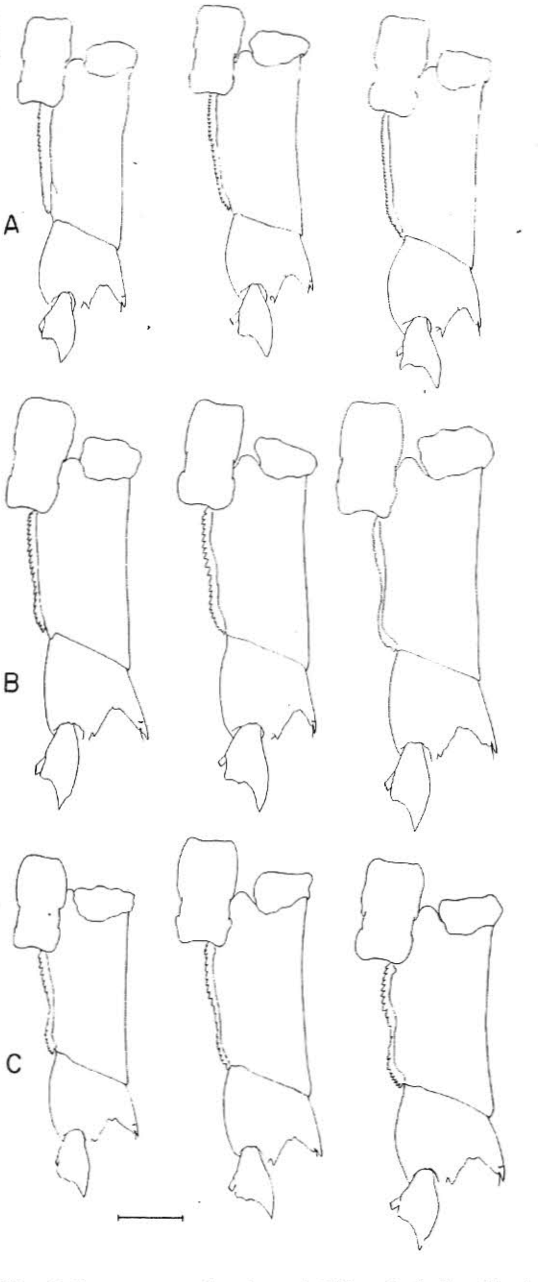

Fig. 10. *Calanus*. Basipod amd Ri1 of left P5 (anterior view) for adult female *C. finmarchicus* (A), *C. glacialis* (B), and *C. marshallae* (C)

some length, which is given by the coefficient of variation, is approximately the same for sympatric and allopatric populations. Thus, there is no suggestion in these data of bias in the separation of individuals among the two species when they are sympatric. By including measurements on specimens from all other plankton samples containing these species, the length range of each species was expanded somewhat (Table 3).

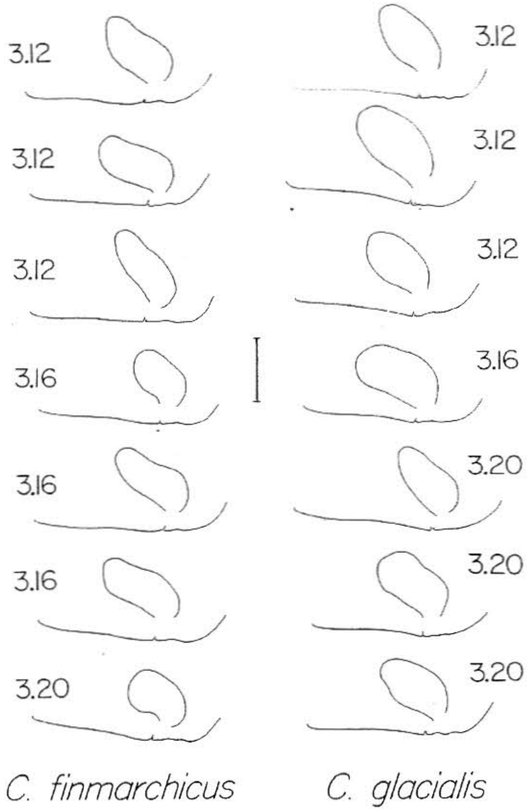

Fig. 11. *Calanus*. Ventral portions of genital segments (right lateral view) showing variability in size, shape and orientation of seminal receptacle in adult female *C. finmarchicus* (left column) and *C. glacialis* (right column). All specimens are similar in size (prosome lenght, in mm, is given for each) and all were taken from one plankton sample (Greenland Sea, Latitude 67° 12'N; Longitude 25°34'W; May, 1965)

Table 3. *Calanus finmarchicus* species group. Range of total length (TL, mm) and prosome length (PL, mm) of adult females and males. These data represent extremes of length measurements found in all of material (see sections on material examined for numbers of specimens on which ranges are based)

		C. finmarchicus	*C. glacialis*	*C. marshallae*
Adult female	TL	2.42–4.21	3.60–5.46	2.89–4.52
	PL	1.95–3.28	2.77–4.34	2.30–3.59
Adult male	TL	2.57–3.98	3.90–5.36	3.28–4.24
	PL	2.08–3.16	2.98–4.18	2.56–3.40

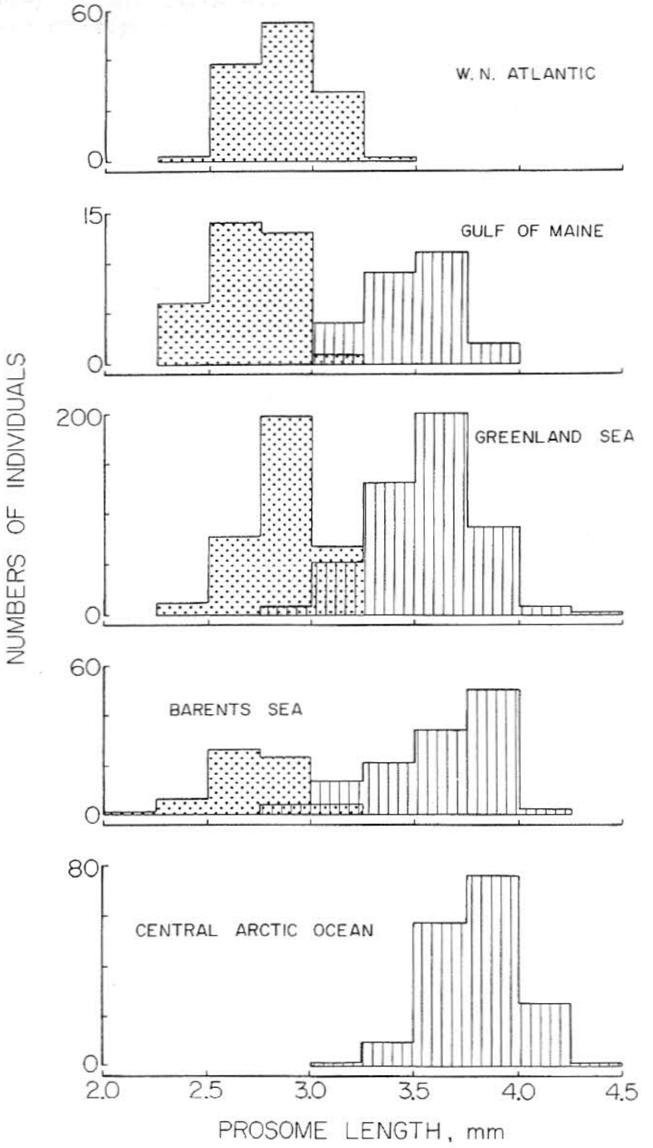

Fig. 12. *Calanus*. Length (prosome)-frequency histograms for females in allopatric and sympatric populations of *C. finmarchicus* (stippled) and *C. glacialis* (vertical hatching). (See Table 2)

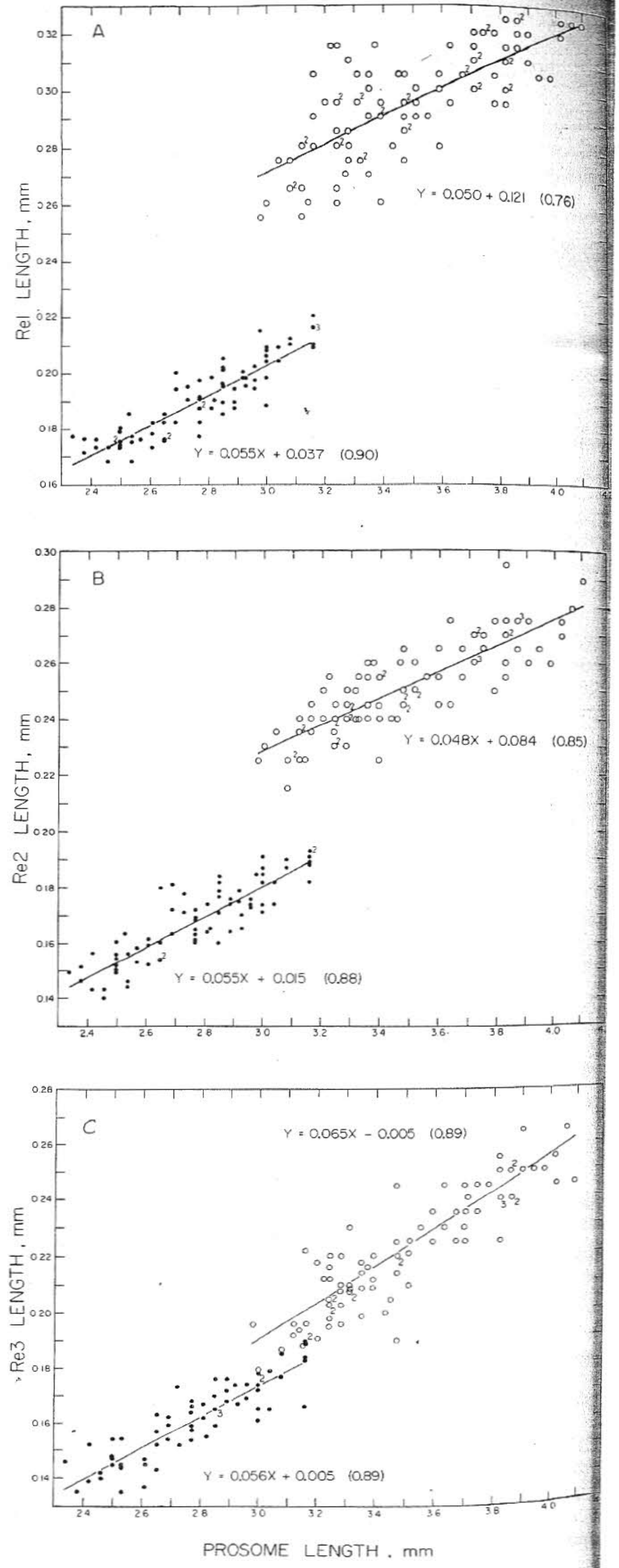

Fig. 13. *Calanus*. (A) Length of Rel of male P5 plotted against prosome length (symbols as in Fig. 8). (B) Length of Re2 of male left P5 plotted against prosome length; data in (A) and (B) from Frost (1971) with some additional measurements, especially of small males of *C. glacialis*. (C) Length of Re3 of male right P5 plotted against prosome length. Slopes of all regression lines differ significantly from zero ($P < 0.001$ for all 6 lines)

Adult Male. The primary characteristics distinguishing males of *Calanus finmarchicus* and *C. glacialis* are the relative lengths of Re1 and Re2 of the left P5; the two species form non-overlapping clusters when lengths of either segment are plotted against prosome length (Fig. 13A,B). Only these two segments differ significantly between the species; the lengths of all other segments of the P5, when plotted against prosome length, show relatively smooth intergradation or extensive overlap between the two species (e.g. Fig. 13C; see also Frost, 1971, Figs. 3 and 4). Thus, the diagnostic mensural difference in Re1 and Re2 between the species is reflected in the relative lengths of the entire left exopod and endopod of the P5 (Jaschnov, 1955, 1957a). In *C. finmarchicus*, the outer distal pointed process of the left Ri2 reaches to or beyond the distal margin of Re1 and the outer distal corner of the left Ri3 extends to or beyond the mid-length of Re2 (Fig. 14A). By contrast, in *C. glacialis*, the outer distal pointed process of the left Ri2 does not usually reach the distal margin of Re1 and the outer distal corner of Ri3 does not reach the mid-length of Re2 (Fig. 14B). Also, with reference to the P5, the spiniform process on Bp2, the outer distal corner of Ri1, and the curvature of the medial margin of Bp2 (Fig. 14) are as described for the females; contrary to the females, there is no apparent difference between the species in the curvature of the medial margin of Bp1. Adult males of the two species overlap in size much more rarely and much less extensively in an area of sympatry than do adult females (Fig. 15), so that in practice, length measurements alone will usually separate the species (Table 3).

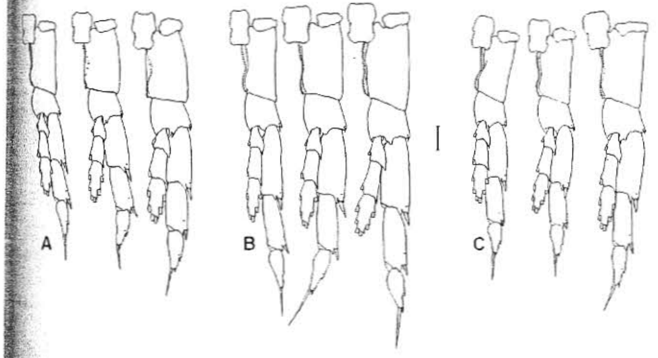

Fig. 14. *Calanus*. Left P5 (anterior view) for adult male *C. finmarchicus* (A), *C. glacialis* (B), and *C. marshallae* (C)

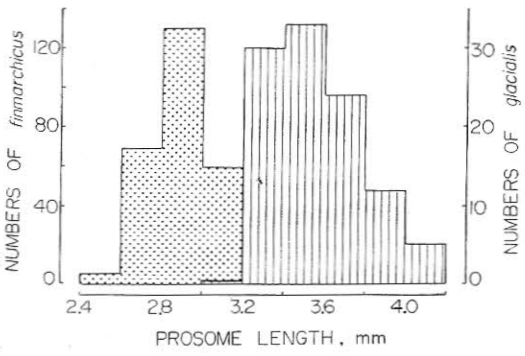

Fig. 15. *Calanus finmarchicus* and *C. glacialis*. Length (prosome)-frequency histogram for adult males collected at several stations in Greenland Sea (March-May, 1965). Note that frequency scales are different for the two species. Number of specimens measured: 262 *C. finmarchicus*, 105 *C. glacialis*

Material Examined and Geographical Distribution. My material, mounted on slides and sorted to species, consists of: 1781 adult females and 1023 adult males of *Calanus finmarchicus*; 1412 adult females and 202 adult males of *C. glacialis*. While this material does not extend the geographical range of either species (see Jaschnov, 1970), the distribution of *C. glacialis* in the North Pacific Ocean can be redefined. In my samples, this species was confined to the large inland seas and continental waters of the western North Pacific Ocean and shallow waters of the Bering Sea, including the broad continental shelf in the eastern and northern Bering Sea; *C. glacialis* was not seen anywhere in the eastern North Pacific south of the Aleutian Islands, although it does extend farther southward of those latitudes along the continental margin of the western North Pacific Ocean (Jaschnov, 1970). The mid-Pacific locality records for *C. glacialis* provided by Park (1968) were puzzling, since the two species of the *C. finmarchicus* group present in the North Pacific Ocean were found by me and other investigators (Brodsky, 1965; Jaschnov, 1970) only in waters bordering the continents and near the Aleutian Islands. It appears that Park's samples actually contained *C. sinicus* (superficially similar to *C. glacialis*, but a member of the *C. helgolandicus* species group) expatriated in the North Pacific Drift far from the apparent center of its geographical range in the Sea of Japan and East China Sea (Brodsky, 1965). Park's description and illustrations of his material conform with *C. sinicus* and, further, I found *C. sinicus* at several mid-ocean localities in the North Pacific Ocean (between Latitude 33°20'N and 42°30'N; Longitude 171°49'W and 168°01'E).

Reference Specimens. Since type specimens of *Calanus finmarchicus* and *C. glacialis* apparently do not exist, series of reference specimens of both species were established in two repositories, the United States National Museum (USNM) and the British Museum of Natural History (BMNH). *C. finmarchicus*: 10 adult females, 9 adult males (66°N 2°E; 4 July, 1952), USNM 142063 and USNM 142064; 10 adult females, 10 adult males (66°N 2°E; 4 July, 1952), BMNH 1972.11.13.3 and BMNH 1972.11.13.4. *C. glacialis*: 10 adult females, 10 adult males

(85°08'N; 88°38'W; 26 April, 1971), USNM 142065; 8 adult males (85°08'N; 88°38'W; 26 April, 1971), BMNH 1972.11.13.6.

Remarks. The great morphological similarity of *Calanus finmarchicus* and *C. glacialis* has provided a severe test for the application to them of traditional approaches utilized in taxonomy of calanoid copepods. Taxonomists rely heavily on the P5 to distinguish many closely related species of calanoids — and with justification, for in most calanoid genera this appendage exhibits strong secondary sexual modification which is often species-specific. However, there are notable exceptions in which the P5 displays significant morphological divergence only at the level of species group or even genus. Thus, for example, over-reliance on the P5 as a source of specific taxonomic characters led to the recognition of only 6 of the 13 species of *Clausocalanus* before that genus was revised by Frost and Fleminger (1968).

While significant differences between *Calanus finmarchicus* and *C. glacialis* reside in the structure of the P5, the differences are subtle and some provide only a statistical basis for inferences about the status of the species. Past uncertainty concerning the two species was brought about, in general, by overemphasis on poorly understood and improperly documented characteristics of the adult female and, specifically, by too narrow, or even erroneous, interpretations based on morphology of the female P5. The study of the female P5 by Aurich (1966) is unsatisfactory because he did not consider variation in the P5 related to body size. Matthews (1967) obtained results on curvature of Bp1 of the P5 which could not be duplicated by later workers (Jaschnov, 1972; this study). In fact, the view, shared by Aurich (1966), Matthews (1967) and Brodsky (1972), that *C. finmarchicus* and *C. glacialis* are subspecies is not substantiated when the characters which they used are examined by the simple statistical presentations given in this report. More significantly, knowledge of the adult males, first provided by Jaschnov (1955, 1957a) and documented more fully by Frost (1971, and in this report), has always been inconsistent with the view that *C. finmarchicus* and *C. glacialis* represent a single variable species. Even Jaschnov (1972), the author of the name *C. glacialis*, mistakenly inferred from observations on the curvature of Bp1 of the female P5 that the two species hybridize where they co-occur. Yet, Jaschnov's data are in close agreement with my results which show that *C. finmarchicus* and *C. glacialis* do not smoothly intergrade in this character. Since, in effect, Jaschnov relied wholly on this character to distinguish similar-sized females of the two species, he had to conclude that specimens intermediate in the character represented rare interspecific hybrids. Now that females of the two species can always be distinguished by other, independent characters (shape of the posterolateral margin of TV and shape of the ventral surface of the genital segment), the curvature of Bp1 of the P5 has been demonstrated to have less significant status as a supraspecific character. Jaschnov also erred, in part, by thinking that allopatric populations of *C. finmarchicus* and *C. glacialis* do not overlap in size; thus, intermediate-sized specimens from regions of sympatry were considered hybrids by him. However, in the regions represented in my material where each species occurs alone, the ranges of size of females of the two species do, indeed, overlap (Table 4, Fig. 12). Thus, there is no logical basis for inferring interspecific hybridization either from geographical variation in size or, as shown above, from other morphological details.

Table 4. *Calanus finmarchicus* and *C. glacialis*. Range of prosome length of adult females in allopatric populations. Length ranges are based on all specimens in material collected from these localities: Norwegian Sea (66°N; 2°E), Western North Atlantic (53°10'N; 45°31'W), Central Arctic Ocean (4 Ice Island T-3 stations in central Arctic Basin, see Fig. 1), and Western North Pacific Ocean and Bering Sea (16 stations among those shown in Fig. 1)

Calanus species	Locality	Range of prosome length (mm)	Number of specimens
C. finmarchicus	Norwegian Sea	2.11-3.12	685
	Western North Atlantic Ocean	2.38-3.28	123
C. glacialis	Central Arctic Ocean	2.98-4.34	524
	Western North Pacific Ocean and Bering Sea	2.81-4.06	101

Calanus marshallae n. sp.

This species is most easily characterized by describing it in direct comparison with *Calanus fi* *marchicus* and *C. glacialis*.

Adult Female. The new species and *Calanus glacialis* are very similar in body form, including the outline of the ventral surface of the genital segment in lateral view and the shape of the posterolateral margin of the TV (Fig. 4C). These fe tures immediately distinguish *C. marshallae* from *C. finmarchicus*. In sharp contrast to both *C. finmarchicus* and *C. glacialis*, the accessory photoreceptor is relatively much larger in *C. marshallae* (Fig.2C); this diagnostic difference is evident in immature stages (Copepodid III-V) as well (Fig. 16). The caudal ramus length in *C. marshallae* is approximately twice the caudal ramus width, but less than the width of the anal segment; in both *C. finmarchicus* and *C. glacialis* the length of the caudal ramus is usually more than twice the width of the caudal ramus and about equal to the width of the anal segment (Fig. 17).

The second maxilla of *Calanus marshallae* nearly always (50 of 51 randomly selected specimens) has a circular cluster of wide, flat, hyaline spinules on the outer proximal surface; this surface on the second maxilla of *C. finmarchicus* and *C. glacialis* is usually devoid of spinules (43 of 51 specimens of *C. finmarchicus*, 37 of 45 specimens of *C. glacialis*) or, if present, the spinules are slender and minute (Fig. 18). In all 3 species, the denticulate medial margin of Bp1 of P5 has a variable number, spacing and size of denticles, so that the species cannot be routinely identified by these characters. Nevertheless, there is a clear statistical trend in the number of denticles on the Bp1, with *C. marshallae* having the lowest average number and *C. finmarchicus* having the highest (Table 1). *C. marshallae* also exhibits a unique pattern in a combination of other features found on the P5. The medial denticulate margin of the Bp1 in *C. marshallae* is usually markedly concave, so that the species is indistinguishable from *C. glacialis* in this (Figs. 10 and 19A). Also, like *C. glacialis*, the spiniform process on the distal anterior margin of Bp2 of *C. marshallae* is thick and blunt on the right or left leg and the outer distal corner of Ri1 is usually narrowly tapered

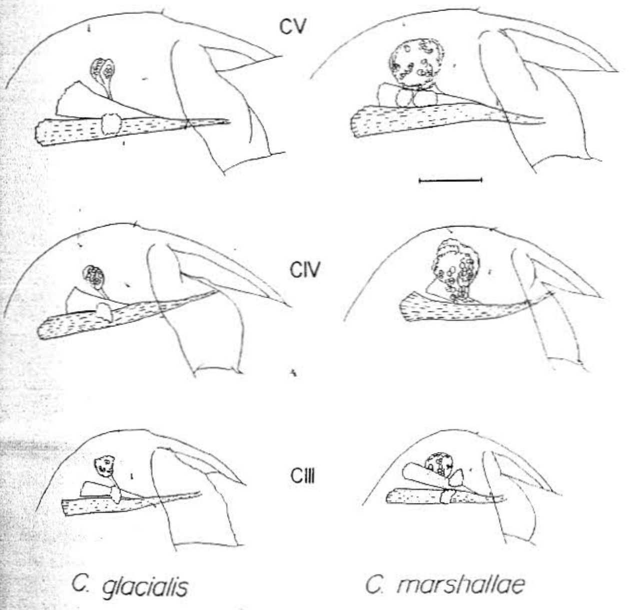

Fig. 16. *Calanus glacialis* and *C. marshallae*. Foreheads (right lateral view) of copepodid stages (CIII, CIV, CV). Immature stages of *C. finmarchicus* are similar to *C. glacialis*

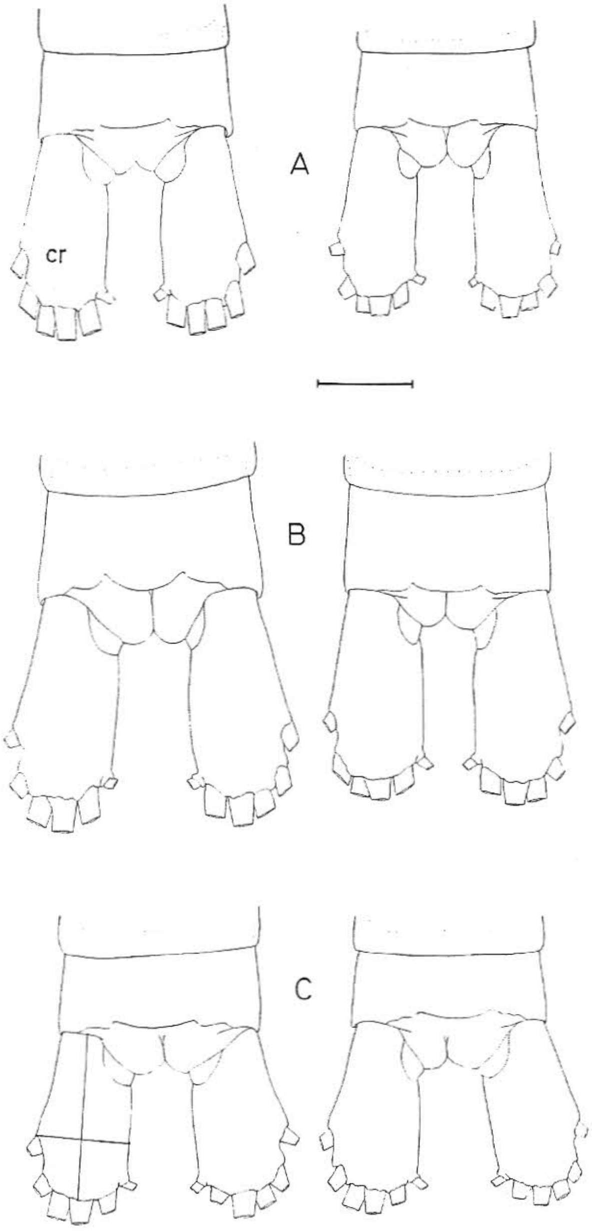

Fig. 17. *Calanus*. Anal segment and caudal rami (cr, dorsal view) for adult females of (A) *C. finmarchicus*, (B) *C. glacialis*, (C) *C. marshallae*. Lines on caudal ramus in lower left figure show limits of the length and the width measurement

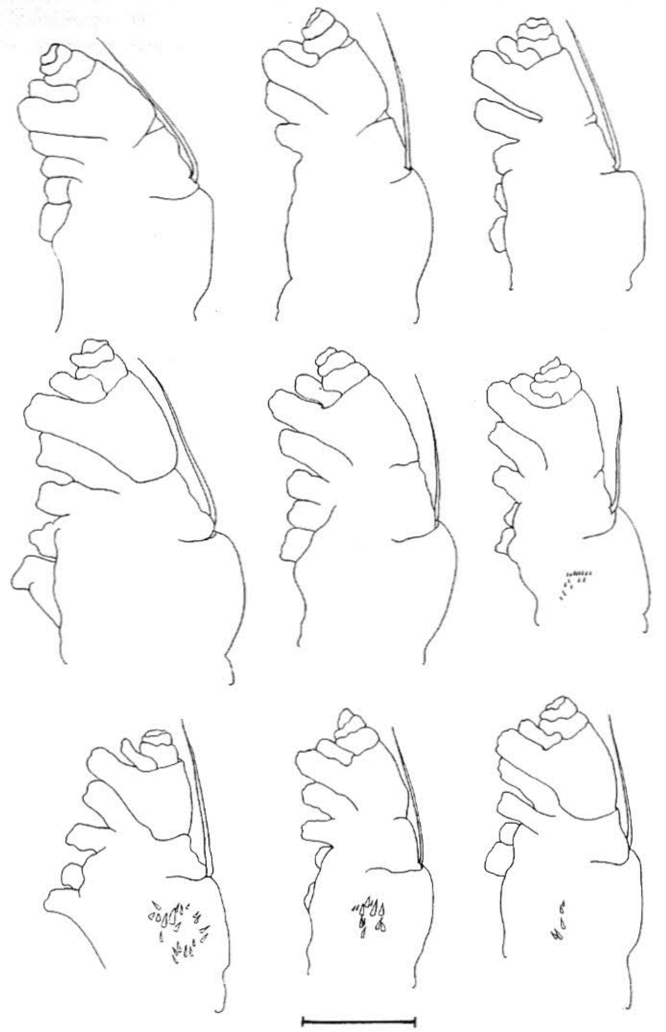

Fig. 18. *Calanus*. Right second maxilla (right lateral view) for adult female *C. finmarchicus* (top row), *C. glacialis* (middle row), and *C. marshallae* (bottom row)

and sharply pointed (Fig. 10). However, in contrast to *C. glacialis*, the medial margin of Bp2 in *C. marshallae* tends to be convex, although not so curved as in *C. finmarchicus* (Figs. 10 and 19B). Thus, the P5 index (see p. 85) for *C. marshallae* is intermediate between those of *C. finmarchicus* and *C. glacialis* (Fig. 19C).

The length range of the adult female of *Calanus marshallae* broadly overlaps those of *C. finmarchicus* and *C. glacialis*, so that the average *C. marshallae* female is intermediate in size between them (Table 3).

Adult Male. The form of the body of the new species is very similar to that of *Calanus finmarchicus* and *C. glacialis*. However, as in the fe-

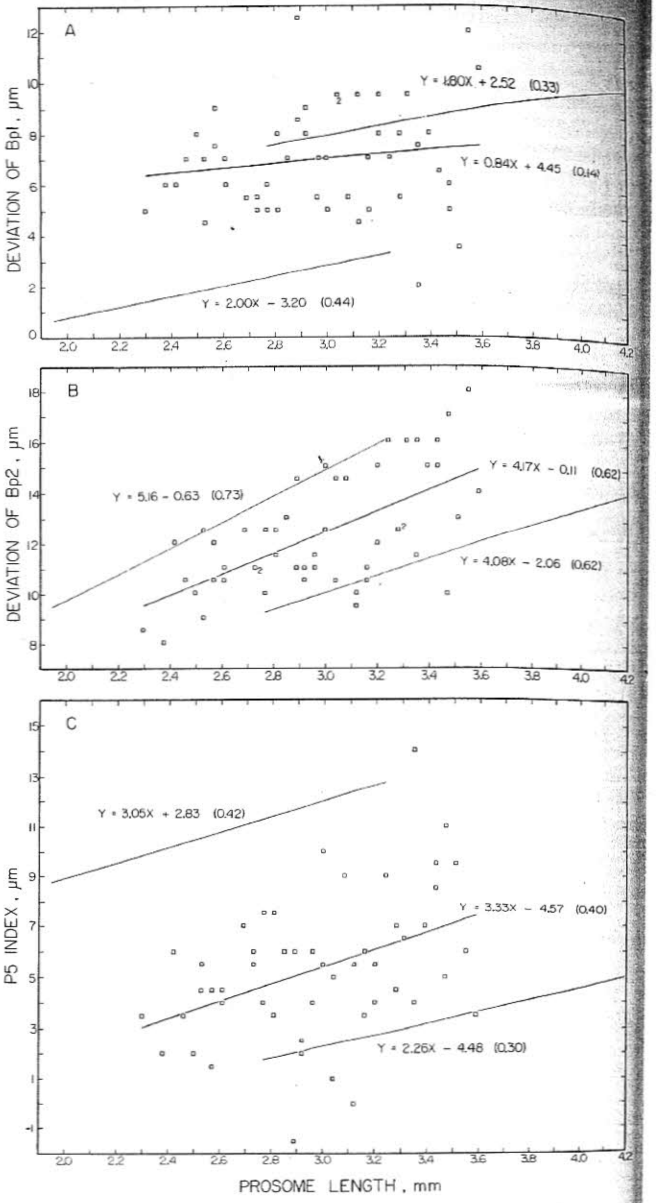

Fig. 19. *Calanus*. (A) curvature (deviation) of medial margin of Bp1 of female P5 plotted against prosome length (open squares, *C. marshallae*); thin lines are regression lines for *C. finmarchicus* (lower line) and *C. glacialis* (upper line) based on the data from Series A and B combined (Fig. 8). Slopes of both regression lines differ significantly from zero ($P < 0.001$ for both); thick line is regression line for *C. marshallae*, slope of this line does not differ significantly from zero ($P \sim 0.3$). (B) curvature (deviation) of medial margin of Bp2 of female P5 plotted against prosome length (symbols and lines as in A). Slopes of all 3 regression lines differ significantly from zero ($P < 0.001$ for all three). (C) P5 index plotted against prosome length (symbols and lines as in A); slopes of all 3 regression lines differ significantly from zero ($P < 0.001$ for all 3)

male, the accessory photoreceptor is very large and immediately distinguishes *C. marshallae* from both *C. finmarchicus* and *C. glacialis* (Fig. 3). The structure of the P5 is intermediate between *C. finmarchicus* and *C. glacialis*, although tending toward the former (Fig. 14), but the lengths of Re1 and Re2 fall along distinct regression lines when plotted against prosome length (Fig. 20A,B). The significance of these differences in lengths of Re1 and Re2 among the three species is highlighted by the lack of similar displacements in length measurements of any other basipodal, exopodal or endopodal segment of the right or left P5 when plotted against prosome length (e.g. Fig. 20C). Because in Fig. 20A,B the lengths of Re1 and Re2 of *C. marshallae* overlap both *C. finmarchicus* and *C. glacialis*, there is no mensural characteristic of the P5 which can be used absolutely to distinguish adult males of *C. marshallae* from the two species. In the P5 the spiniform process on Bp2, the outer distal corner of Pi1, and the curvature of the medial margin of Bp2 (Fig. 14) are as described for the female. As in the female, the length range of the male of *C. marshallae* broadly overlaps those of *C. finmarchicus* and *C. glacialis* (Table 3).

Material Examined and Geographical Distribution. I sorted and examined 585 adult females and 225 adult males of *Calanus marshallae*. The geographical distribution of *C. marshallae* appears centered in the eastern North Pacific Ocean (waters bordering the Gulf of Alaska), in waters adjacent to the Aleutian Islands, and in the eastern Bering Sea (Fig 21). From published distributions of the *C. finmarchicus* species group in the North Pacific Ocean and Bering Sea (Brodsky, 1965; Jaschnov, 1970), it is clear that species of the group are restricted to waters near continental margins, broad continental shelves and shallow seas. Woodhouse (1971) found the southern limit of *C. marshallae* at about Cape Mendocino on the North American coast (Latitude 40°26'N). In the north it appears that *C. marshallae* is swept into the Arctic Ocean through the Bering Strait, but the species was relatively rare in samples from this region.

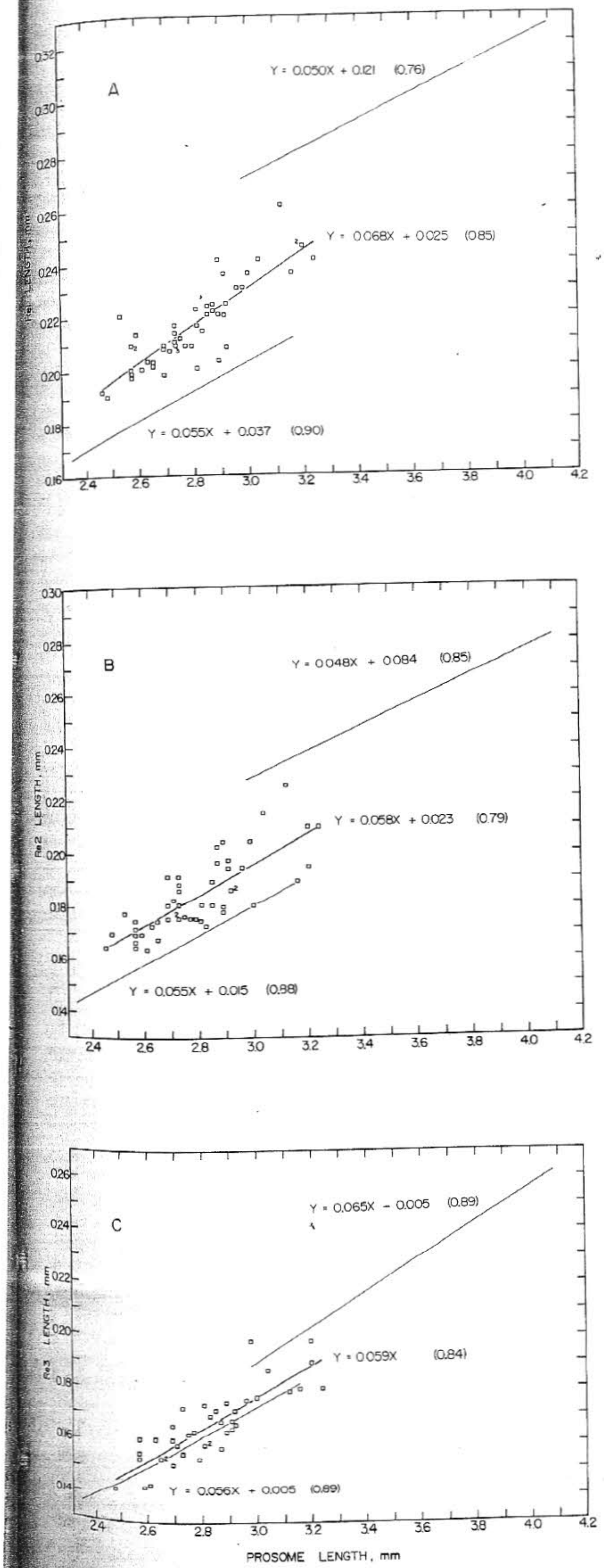

Fig. 20. *Calanus*. (A) length of Re1 of male left P5 plotted against prosome length (open squares, *C. marshallae*); (B) length of Re2 of male left P5 plotted against prosome length (symbols as in A); (C) length of Re3 of male right P5 plotted against prosome length (symbols as in A). In all three graphs, thin lines are regression lines for *C. finmarchicus* (lower line) and *C. glacialis* (upper line) from Fig. 13. Thick line is regression line for *C. marshallae* (other symbols as in Fig. 8). Slopes of all regression lines differ significantly from zero ($P < 0.001$ for all)

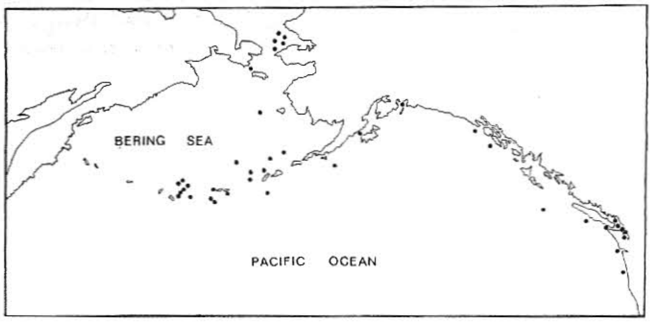

Fig. 21. *Calanus marshallae.* Occurrence in plankton samples shown in Fig. 1. Also indicated in Fig. 1 are the three records of *C. marshallae* near Banks Island

Beyond the immediate area of the Bering Strait a few specimens of *C. marshallae* were found only in the vicinity of Banks Island (Fig. 1). *C. marshallae* and *C. glacialis* occurred together in the 2 samples taken over the broad continental shelf in the eastern Bering Sea and in 5 samples from the region of the Bering Strait.

Types and Reference Specimens. The following type-series is established: holotype, adult female, total length 3.76 mm, USNM 142060; allotype, adult male, total length 3.52 mm, USNM 142061; paratypes, 10 adult females, 10 adult males, USNM 142062, all collected in a 0 to 130 m oblique tow west of Cape Flattery (Washington) at Latitude 48°21'N; Longitude 124°52'W (27 May, 1969). The following paratypes are deposited at the British Museum of Natural History: 10 adult females, 10 adult males, BMNH 1972.11.13.5, from the sample containing the type specimens.

Remarks. Jaschnov (1957b) first hinted that in the eastern North Pacific Ocean there might be an undescribed species of *Calanus* closely related to *C. finmarchicus.* Later, Jaschnov (1970) decided that two forms of *C. glacialis*, a large and a small form, exist in the North Pacific Ocean. The small form to which he refers is, in part, the new species *C. marshallae* and the large form is *C. glacialis.* Jaschnov (1970) also thought that the small form occurred off Japan, but the one reliable work he cites (Tanaka, 1956) deals with *C. pacificus* and *C. sinicus*. *C. marshallae* (as *Calanus* sp.) was analyzed in detail by Shan (1962) and Woodhouse (1971), who were primarily concerned with distinguishing it from *C. pacificus.* All three of the above authors were reluctant to declare that populations of *C. marshallae* are taxonomically distinct from *C. finmarchicus* and, especially, *C. glacialis*. Undoubtedly, this was because the latter two taxa were so poorly defined in the literature. The present analysis has demonstrated that both allopatric and sympatric populations of *C. finmarchicus* and *C. glacialis* are morphologically distinctive.

In many respects, *Calanus marshallae* is a conglomeration of the characteristics of both *C. finmarchicus* and *C. glacialis*. Grossly, the female of *C. marshallae* is most like *C. glacialis*, while the male *C. marshallae* tends toward *C. finmarchicus.* Yet, *C. marshallae* possesses a number of unique characteristics. Of these, the size of the accessory photoreceptor in both sexes is the most prominent; the spinules on the second maxilla and the length-to-width ratio of the caudal ramus are also significant for differentiating females of *C. marshallae* from both *C. finmarchicus* and *C. glacialis*. Further, although the length range of adults of *C. marshallae* extensively overlaps both *C. finmarchicus* and *C. glacialis*, meristic and mensural characteristics known to vary with size of the animal (e.g. number of teeth on Bp1 of the female P5, curvature of the Bp2 of the female P5, and lengths of Re1 and Re2 of the male P5) clearly show that *C. marshallae* is not a simple blend of the features of either of those two species. That is, in scatter diagrams with *C. finmarchicus* and *C. glacialis* the characters of *C. marshallae* form distinct clusters rather than being superimposed completely on either of the other species.

Calanus marshallae and *C. finmarchicus* do not co-occur, although there are a few reliable records of adult females of *C. finmarchicus* in the central Arctic Ocean (Johnson, 1963; one of our records) and *C. marshallae* may be transported north of the Bering Strait. In practice, then, identification of *C. marshallae* will depend solely on those characters, described above, that distinguish it from *C. glacialis*.

Woodhouse (1971) found that *Calanus marshallae* and *C. pacificus* (a species of the *C. helgolandicus* group) co-occur along the west coast of North America approximately between Latitudes 40° and 50°N. In fact, earlier taxonomic studies dealing with the northeastern North Pacific Ocean are generally not reliable because *C. marshallae* and *C. pacificus* were usually grouped. I also found both species in samples taken near the Aleutian Islands. *C. marshallae* and *C. pacificus* are easily distinguished by the species group characters described earlier (see also Woodhouse, 1971) and also by the size of the accessory photoreceptor (all species of the *C. helgolandicus* group are like *C. glacialis* in this character).

Species Name. Calanus marshallae is named in honor of Dr. S.M. Marshall who, together with the late A.P. Orr, pioneered the ecological study of marine planktonic copepods, especially species of the genus *Calanus*.

Discussion

It is not probable that further taxonomic study utilizing the light microscope will yield new external morphological characters to distinguish

Calanus finmarchicus and *C. glacialis*. However, I am confident that novel approaches applied to studies of their taxonomy (e.g. Manwell *et al.*, 1967) will support the several types of evidence now available which indicate that the two taxa represent reproductively isolated populations and are, therefore, valid species. The morphological evidence for this view is presented above. Also, clear differences exist between the species in geographical distribution (Jespersen, 1934, 1939; Wiborg, 1955; Jaschnov, 1961, 1970; Grainger, 1963; Matthews, 1969) and, where they co-occur, in vertical distribution (Jespersen, 1934, 1939; Jaschnov, 1958, 1961). Finally, in sympatric populations of the two species, the timing of their life cycles is quite different (Maclellan, 1967; Matthews, 1969).

This evidence has accumulated slowly. Before Jaschnov's study (1955), *Calanus finmarchicus* and *C. glacialis* were regarded as large and small forms of *C. finmarchicus*. Hence, bimodal length-frequency distributions with well separated modes (e.g. Fig. 12) were frequently described for samples of adult *Calanus "finmarchicus"* collected in the North Atlantic Ocean. The apparent lack of morphological differences between the large and small forms led many workers to conclude that the two forms represented a single variable species (e.g. Mrazek, 1902; Størmer, 1929; Jespersen, 1934, 1939; Ussing, 1938; Digby, 1954; Wiborg, 1955).

As I pointed out (Frost, 1971), no compelling argument has been advanced to account for the environmental induction of such bimodal length-frequency distributions; the problem is that both modes represent mature specimens of *Calanus*. Bimodal size-frequency distributions are fairly common in Arctic species of zooplankton with long generation times (Dunbar, 1940), but in every case the modes represent different generations, that is, the small mode represents immature specimens and the large mode mature specimens. Nevertheless, Aurich (1966) and Matthews (1967) believe that *Calanus finmarchicus* and *C. glacialis* are ecophenotypes, differing only in size, of an arcto-boreal species (see Ekman, 1953). Differences in size observed between the two ecophenotypes when they co-occur in the subarctic zone (mixed boreal and Arctic water; see Dunbar, 1968) are acquired, according to Aurich and Matthews, in populations originating from pure boreal and pure Arctic waters. Thus, in samples of *C. "finmarchicus"* with bimodal length-frequency distributions, the small mode characterizes individuals of boreal zone origin while the large mode typifies individuals of Arctic zone origin. In Matthews' view, the relatively rare intermediates between co-occurring boreal and Arctic phenotypes arise in the geographically restricted subarctic zone. My results, showing differences, independent of size, between *C. finmarchicus* and *C. glacialis* obviate the need for accounting for intermediates in body size by this mechanism. Merely the fact that allopatric populations of *C. finmarchicus* and *C. glacialis* overlap in body size (Table 4) refutes Matthews' theory. Further, it should be noted that the geographical distribution of *C. finmarchicus* s.str. (see Jaschnov, 1970) is not unique; a number of taxonomically well known planktonic species have similar distributions in the North Atlantic Ocean (Table 5). Other planktonic species have distributions similar to that of *C. glacialis* (Table 5). Finally, bimodal size-frequency distributions of mature specimens have not been reported for other well known planktonic species with true arcto-boreal distributions (Table 5) and having generation times comparable to those of *C. finmarchicus* and *C. glacialis*. Body size in at least one of the arcto-boreal species, *Sagitta elegans*, varies markedly with latitude (Alvariño, 1965).

Species of the *Calanus finmarchicus* group occurring in the North Pacific Ocean have received much less attention than those in the North Atlantic Ocean. The taxonomic problem has actually been more complex in the North Pacific Ocean because often the two species of the *C. helgolandicus* group which occur there (*C. pacificus* and *C. sinicus*) were identified as *C. finmarchicus* or *C. glacialis*. This confusion should no longer arise, since members of the *C. helgolandicus* and *C. finmarchicus* species groups can always be distinguished by (1) relative lengths of Re1 and Ri1 of the P5; (2) development of spiniform process on Bp2 of P4 and P5. Nevertheless, because of earlier

Table 5. Some planktonic animals with geographical distribution similar to those of *Calanus finmarchicus* (boreal) and *C. glacialis* (Arctic) in the North Atlantic Ocean and Arctic Ocean; also included are 3 examples of planktonic animals with arcto-boreal distributions

Distribution	Species	Source
Boreal	*Euchaeta norvegica*	Edinburgh (1973)
	Metridia lucens	Edinburgh (1973)
	Parathemisto gaudichaudii	Bowman (1960)
	Meganyctiphanes norvegica	Dunbar (1964)
	Thysanoessa longicaudata	Dunbar (1964)
	Spiratella retroversa	Spoel (1967)
Arctic	*Metridia longa*	Edinburgh (1973)
	Parathemisto libellula	Bowman (1960)
Arcto-boreal	*Clione limacina*	Spoel (1967)
	Spiratella helicina	Spoel (1967)
	Sagitta elegans	Alvariño (1965)

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Calanus marshallae, a New Species of Calanoid Copepod Closely Allied to the Sibling Species *C. finmarchicus* and *C. glacialis**

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Abstract

Species of the copepod genus *Calanus* frequently dominate the marine zooplankton in boreal and arctic waters. Up to now there have been no operational means of identifying several species closely related to *Calanus finmarchicus*. Reanalysis of these taxa, using material from plankton samples collected throughout Northern Hemisphere polar and boreal waters, shows that there are 3 sibling species which have been previously combined under the names *C. finmarchicus* and *C. glacialis*. Several new taxonomic characters permit unequivocal identification of *C. finmarchicus, C. glacialis,* and a new species, *C. marshallae*. Claims that *C. finmarchicus* and *C. glacialis* are subspecies are refuted; there is no evidence that the two species continuously intergrade either where they co-occur or where they are allopatric, nor is there evidence that the two species hybridize. *C. finmarchicus* is basically restricted to the North Atlantic Ocean and *C. marshallae* to the North Pacific Ocean and Bering Sea; *C. glacialis* is primarily an Arctic species, but its geographical distribution slightly overlaps those of the other two species. Taxa closely related to *C. finmarchicus* and *C. helgolandicus* probably represent two separate, but closely linked evolutionary lineages; species of these two lineages are placed in one of two species groups, the *finmarchicus* group and the *helgolandicus* group.

Introduction

During the process of species formation in sexually reproducing organisms, reproductive isolation between populations or groups of populations may be achieved with varying degrees of morphological divergence. Two or more species which in the extreme are nearly identical morphologically are called sibling species by Mayr (1963). Sibling species, while problematical for classifiers of nature (see Sokal and Crovello, 1970), have special significance for students of evolution (Dobzhansky, 1972). Further, ecological studies of sympatric sibling species may elucidate how species interact, utilize resources and partition the environment.

Cases of sibling species among numerically dominant groups of marine planktonic calanoid copepods are well documented. Good examples are found in the three species groups of *Clausocalanus* (Frost and Fleminger, 1968) and the pair of species *Calanus tenuicornis* and *C. lighti* (Bowman, 1955; Mullin, 1969). The genus *Calanus* also contains a taxonomically less well delimited complex of sibling species, including the North Atlantic species *C. finmarchicus* (Gunnerus, 1765) and *C. helgolandicus* (Claus, 1863). Although Sars (1901) redescribed *C. finmarchicus* and distinguished it from *C. helgolandicus,* his opinion was not universally accepted, for while adult males of *C. finmarchicus* and *C. helgolandicus* were never confused (Sars, 1901; Rees, 1949), adult females seemed to possess no non-intergrading morphological characteristics (see Rose, 1933). Discussion of the validity of these species has persisted to the present (cf. Aurich, 1966; Manwell *et al.,* 1967; and Matthews, 1967). Despite this uncertainty, Brodsky (1948) proposed the new name *C. pacificus* for populations morphologically very similar to *C. helgolandicus,* but geographically separated from it in the North Pacific Ocean, and Jaschnov (1955) gave the new name *C. glacialis* to Arctic populations which possess morphological attributes very like those of *C. finmarchicus*. Fleminger (1964) argued that the comparatively minor morphological differences between *C. helgolandicus* and *C. pacificus* and the relatively recent, possibly short-lived, geographic separation of these taxa did not warrant assigning them separate specific names. Also, for reasons outlined later in this paper, the validity of *C. glacialis* is currently under debate (Grainger, 1961; Aurich, 1966; Matthews, 1966, 1967; Frost, 1971; Brodsky, 1972; Jaschnov, 1972).

My interest in *Calanus finmarchicus* and *C. glacialis* stems from study of a closely related species occurring in the eastern North Pacific Ocean and eastern Bering Sea. This species, while morphologically quite similar to *C. finmarchicus* and *C. glacialis* (Shan, 1962; Jaschnov, 1970; Woodhouse, 1971), conforms with published descriptions of neither species. Obviously, another species

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confusion and less intensive investigation, there is little reliable data in the literature from which to compare, for example, vertical distributions and life cycles of *C. glacialis* and *C. marshallae* in the North Pacific Ocean. These two species co-occur only in the eastern and northern Bering Sea, and virtually nothing is known about the seasonal cycles of plankton populations in that region. It can, however, be asserted that in the 7 samples in my material which contained both species, the species were always easily distinguished.

The relatively slight degree of morphological divergence among species of the *Calanus finmarchicus* group is striking in comparison with other groups of calanoid copepods. However, sibling species seem to be unusually numerous in the genus *Calanus*. The sibling species of the *C. helgolandicus* group (Brodsky, 1965) promise to be even more challenging to taxonomists than those of the *C. finmarchicus* group, especially since many of the *C. helgolandicus* species do not co-occur. *C. lighti* and *C. tenuicornis* differ only in body size and one other small morphological detail (Bowman, 1955). Common to all of these examples, with two partial exceptions *(C. finmarchicus* and *C. glacialis)*, is the remarkable similarity within a species group of the male P5. As pointed out earlier, copepod taxonomists have come to regard the male P5 as one of the most dependable taxonomic characters for distinguishing closely related species. Secondary sexual modification is especially pronounced in the appendage, suggesting that genetic divergence during speciation finds its greatest phenotypic expression here. Since in many groups of calanoids the P5 is used by the male to grasp the female during mating (see Fleminger, 1967; Roff, 1972), it is tempting to infer that interspecific differences in the P5 reflect reinforcement, via natural selection, of interspecific reproductive isolation by mechanical incompatibility. Nevertheless, the relatively great similarity of the male P5 in the above-mentioned species groups of *Calanus* does not necessarily mean that mechanisms for interspecific reproductive isolation are weak. On the contrary, as Frost and Fleminger (1968) suggested for *Clausocalanus*, reproductive isolation among closely related species of *Calanus* may be accomplished in several other ways. One obvious mechanism, already documented for *C. finmarchicus* and *C. glacialis*, is different phasing of reproductive cycles where species co-occur. Vertical separation of species could also be effective in isolating breeding populations of two co-occurring species. Finally, there may be more subtle mechanisms, such as interspecific differences in mating behavior or in chemical recognition systems (Fleminger, 1967). Katona (1973) describes "mate-seeking behavior" for adult males of three species of planktonic copepods, and suggests that the behavior is elicited by pheromones originating from adult females. Also, Griffiths and Frost (in press) have observed sex-specific patterns of swimming, presumably part of mating behavior, in *Calanus pacificus* and *Pseudocalanus* sp., and have demonstrated that pheromones are utilized for intraspecific communication between sexes.

Although in the past there was considerable confusion about the taxonomic status of *Calanus finmarchicus* and *C. helgolandicus*, there is now substantial indication that these species belong to separate, probably recently divergent, evolutionary lineages. Today both lineages are represented by several sibling species, each with slightly overlapping or distinct geographical distribution. While it appears that the *C. helgolandicus* group needs further study, the *C. finmarchicus* group is sufficiently known that the pattern of distributions of its sibling species suggests a scheme for speciation within the group. Jaschnov (1958) thinks that *C. glacialis* recently derived from *C. finmarchicus*; now that a third species is recognized in the group, another alternative can be suggested. Over major portions of their ranges, each species of the *C. finmarchicus* group occurs alone. Thus, *C. finmarchicus* is the boreal North Atlantic species, *C. marshallae* occupies a somewhat analogous, but more restricted, habitat in the North Pacific and Bering Sea, and *C. glacialis* is essentially interposed between them in the Arctic Ocean. In the past a single precursor species of the *C. finmarchicus* group, probably similar to *C. glacialis*, may have ranged throughout high-latitude oceans of the Northern Hemisphere presently occupied by the group. Such distributions are known today (e.g. that of *Spiratella helicina*, Table 5). Assuming that geographical isolation is a prerequisite for speciation in sexually reproducing planktonic organisms, breakup of the precursor population into two isolated populations, a North Pacific-Bering population and an Arctic-North Atlantic population could be accomplished by emergence of the Bering Strait land bridge. The land bridge is known to have submerged and emerged a number of times during the Quaternary (Hopkins, 1967) but closure of the Atlantic Ocean-Arctic Ocean connections during this period is highly unlikely. Thus, species of the *C. finmarchicus* group must have originated in at least two cycles of isolation and reinvasion. In the first cycle, the *C. glacialis*-like precursor and its geographical isolate in the North Pacific-Bering Sea may have given rise, respectively, to *C. glacialis* and *C. finmarchicus*. After submergence of the land bridge during an interglacial stage, *C. finmarchicus* could have reinvaded Arctic waters and spread into the North Atlantic Ocean. This would probably require considerably different, perhaps warmer, climatic conditions than prevail today and could have caused the retreat of *C. glacialis* from the North Pacific and Bering Sea into the central Arctic Basin. Reclosure of the Bering land bridge during a subsequent glacial stage could have isolated a population of *C. finmarchicus*, the forerunner of *C. marshallae*, in the North Pacific-Bering Sea from populations of *C. glacialis* and *C. finmarchicus* in the Arctic Ocean and North Atlantic Ocean. Cool climatic conditions during later interglacials, comparable to the present climate, may have prevented *C. marshallae* and *C.*

nmarchicus from redispersing through the Arctic ean, but could have allowed reinvasion of the ring Sea by *C. glacialis*. Obviously, this theory nnot be tested for *Calanus*, but a similar mech- ism might apply to other types of planktonic or- nisms, with distributions similar to those of *lanus*, which leave fossilized remains in the ediments.

The absence of the *Calanus finmarchicus* group n waters over the deep basins of the North Pa- ific Ocean and Bering Sea is puzzling, since over he open boreal North Atlantic Ocean species of he *C. finmarchicus* group are usually among the ost abundant species of zooplankton (Edinburgh, 973). Although there are definite hydrographic ifferences between the two oceans in high north- rn latitudes, within the North Pacific obvious ifferences in hydrographic features (e.g. tem- erature, salinity) are not apparent between con- inental waters where species of the *C. finmarchi- us* group flourish and more offshore waters where hey are absent. By contrast, the North Pacific cean and deep Bering Sea differ biologically from he North Atlantic because of the presence of two ther, presumably herbivorous, species of *Calanus*, *C. cristatus* and *C. plumchrus*. These two species are considerably larger in body size than either *C. glacialis* or *C. marshallae*, and have distinctly different life cycles which apparently lead to profound effects on the primary production cycle (Heinrich, 1962). This and the fact that rather sharp distributional boundaries exist between the *cristatus-plumchrus* assemblage and the *glacialis-marshallae* assemblage (Omori, 1965) suggest that interspecific competitive interactions are, or were, responsible for the geographical restriction of *C. finmarchicus* group species to continental waters of the North Pacific Ocean and Bering Sea. However, here the speculation must cease, for it remains to be revealed why most species of oceanic plankton are not cosmopolitan, especially in view of the absence of physical barriers to dispersal.

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closely related to *C. finmarchicus* and *C. glacialis* cannot be fully documented without first clearing up, as far as possible at this time, the status of these two taxa. Thus, one goal of this paper is to present evidence indicating that *C. finmarchicus* and *C. glacialis* are valid species; having done this, I will show that there are, in fact, 3 sibling species of *Calanus* in the Northern Hemisphere which have been previously combined under the names *finmarchicus* and *glacialis*. The philosophy taken in carrying out this study is that species of copepods represent well integrated, co-adapted groups of genes and that the integrity of the gene pools of species is protected from disruptive interspecific hybridization through interspecific reproductive isolation (see Mayr, 1963). In this study, interspecific reproductive isolation is inferred entirely from morphological evidence.

Material and Methods

The study is based upon material from approximately 140 plankton samples collected throughout Northern Hemisphere polar and boreal waters (Fig. 1). The material covers virtually the entire geographical range of *Calanus finmarchicus* and *C. glacialis* (Jaschnov, 1970); a complete listin of collecting data for the samples as well as th material examined is available from the author.

Specimens were removed from plankton samples and immersed in a 50:50 solution of glycerine and seawater. All illustrations were made from glycerine-mounted specimens using a Wild M20 drawing tube.

To construct length-frequency curves for populations, specimens were removed at random from plankton samples; that is, all specimens were taken in the order in which they were encountered while scanning subsamples mixed homogeneously in a sorting tray.

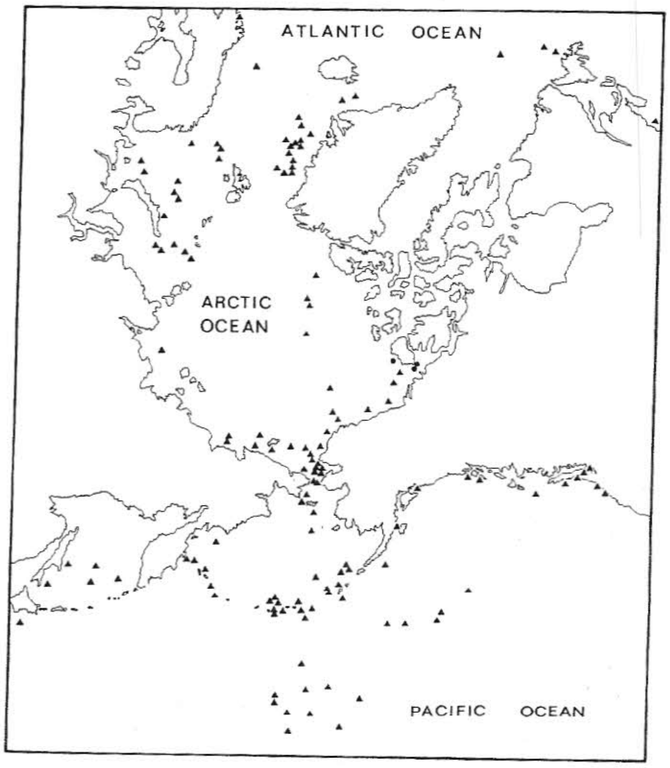

Fig. 1. Distribution of plankton samples utilized in study. Three solid dots near Banks Island represent the only records of *Calanus marshallae*, n.sp., north of immediate vicinity of Bering Strait (see Fig. 21)

Terminology and Taxonomic Characters

Unless otherwise stated, this report deals with adult specimens of *Calanus*. Morphological terminology generally follows that of Fleminger (1967). In *Calanus*, the prosome consists of a cephalosome and a metasome of 5 articulated thoracic segments (TI-TV), each of the latter bearing a pair of swimming legs (P1-P5). The term "forehead" refers to the region of the cephalosome, viewed laterally or dorsally, from the anterior margin at the base of the rostrum to a point on the dorsal surface above the articulation of the mandible (Frost and Fleminger, 1968).

In addition to the usual external morphological characteristics used in taxonomic studies of calanoid copepods, some internal structures are very useful for distinguishing species. Within the forehead of adults of both sexes, there are relatively conspicuous, paired structures located anteriorly and laterally to the antennular muscles and adjacent to the cuticle. Since these structures are not chitinous, their complete description must await the results of histological examination currently being made by Dr. P.L. Dudley; I report here only the gross anatomical features of the structures which are applicable to this taxonomic study. When viewed *in situ* through the intact exoskeleton of the female, 2 structures are evident on either side of the forehead: an anterior body to which a thick, posteroventrally directed nerve is connected and a posterior body (Fig. 2A). From preliminary work, Dr. Dudley (personal communication) believes that the innervated structure is an accessory photoreceptor and it will be referred to by that name. Further, while Dr. Dudley thinks that this is the same structure called "Organ of Gicklhorn" in Elofsson's (1970) study of *Calanus*, she presently prefers to reserve that name for the structure to which it was originally applied in the cyclopoid *Cyclops strenuus*, since homologies have not been definitely established between cyclopoids and calanoids with respect to the organ. Apparently, the posterior body has not been previously described and it will be given the explicitly neutral name "lateral gland" of the forehead. Dr. Dudley suggests that it may be a mucous gland or special oil deposit.

receptor appears histologically under these conditions.

characters are best seen by removing

the body and examining it in anterior view. Each right and left P5 consists of a two-segmented basipod (Bp), a three-segmented exopod (Re) and a three-segmented endopod (Ri). Following Rose (1933), segments of the basipod and each ramus of the P5 are numbered consecutively beginning with the proximal segment; thus the proximal, middle, and distal segments of the exopod are abbreviated Re1, Re2, and Re3, respectively (see Fig. 5). In adult females the P5 is symmetrical and diagnostic features are primarily found in the two basipodal segments (Bp1 and Bp2). The medial margin of Bp1 bears a denticulate border or lamella which extends from the intercoxal plate to near the distal medial corner. The number, size and spacing of denticles on this border are highly variable, but among females of the species treated in this report the degree of curvature of the denticulate border is a significant character. Important characters on Bp2 are the degree of curvature of the medial margin and the size and shape of a small spiniform or knob-shaped process on the distal anterior margin and overlapping the proximal medial corner of Re1 (Fig. 5). In adult males, the P5 is asymmetrical and differences among species are found primarily in the relative lengths of the left Re1 and Re2.

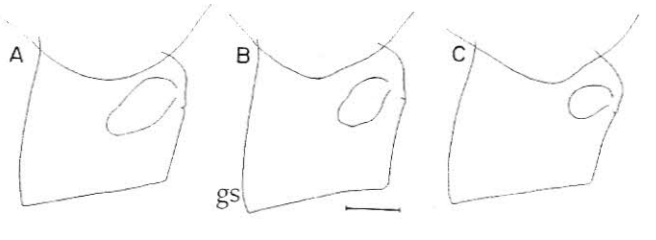

Fig. 4. *Calanus*. Posterolateral margin of TV and genital segment (gs) (right lateral view) for adult females of (A) *C. finmarchicus*, (B) *C. glacialis*, (C) *C. marshallae*

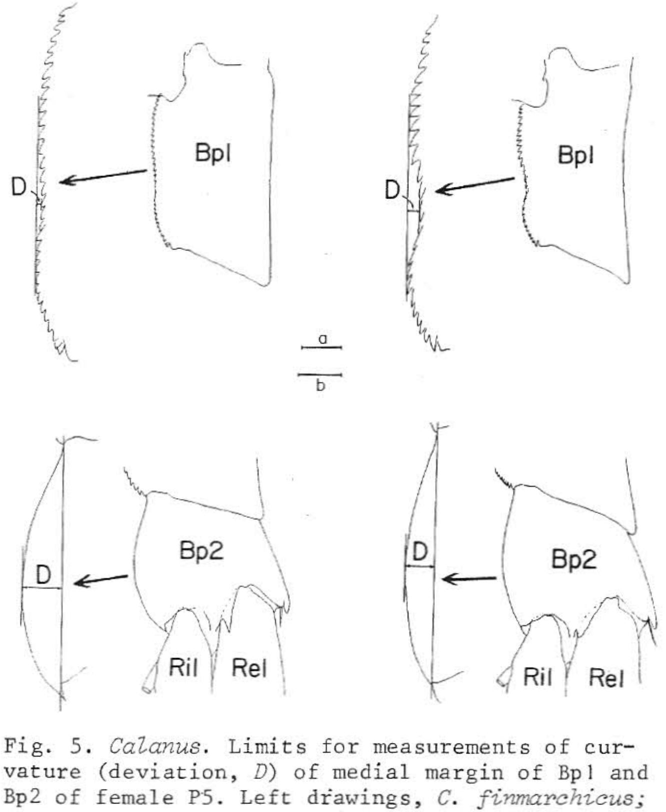

Fig. 5. *Calanus*. Limits for measurements of curvature (deviation, *D*) of medial margin of Bp1 and Bp2 of female P5. Left drawings, *C. finmarchicus*; right drawings, *C. glacialis*. Anterior views. Ri1: first endopodal segment; Re1: first exopodal segment. Scale *a* (0.05 mm) applies to each entire basipodal segment; scale *b* (0.02 mm) applies to enlarged medial margins

Measurement and their Analysis

Measurements were made on specimens mounted in 50:50 glycerine and seawater. Prosome length was measured laterally from the anterior margin of the head to the posterolateral margin of TV. Total length was measured laterally from the anterior margin of the head to the posterior margin of the caudal ramus (excluding caudal setae); only unflexed specimens were used for this measurement and no allowance was made for telescoping segments. Both length measurements were taken at 25X with an ocular micrometer read to the nearest whole micrometer unit (micrometer unit = 0.039 mm). The caudal ramus length was measured dorsally from the anterior margin along the midline to the posterior margin. The width of the anal segment was measured dorsally at the widest point.

For the female, the curvature of the denticulate medial margin of Bp1 of P5 was measured as the deviation from a straight medial margin, by a method similar to that used by Matthews (1967) and Jaschnov (1972). Routinely, the whole P5 of a specimen was removed, mounted anterior side upward on a glass slide, and gently flattened with a glass coverslip; it is not certain that Matthews and Jaschnov treated their specimens in this manner, but it appears that this is the only way to achieve uniform preparation of specimens for comparison of basipods (Woodhouse, 1971). Unlike Matthews (1967), I did not set the limits for the deviation measurement on a particular pair of denticles, but always measured deviation perpendicularly from a straight line connecting the tips of the most medially protruberant proximal and distal denticles to the tip or side of the most depressed denticle located between them (Fig. 5). Hence, negative values were never obtained for this measurement of deviation.

The curvature of the medial margin of Bp2 of the female P5 was also measured, after preparation of the P5 described above, as the deviation from a straight margin. Deviation was taken as the maximum perpendicular distance between the medial margin of Bp2 and a straight line extending from the proximal medial corner of Bp2 to the distal medial corner, which is defined by the distal cuticular margin of Bp2 curving posteromedially from the point of articulation of Ri1 (Fig. 5).

Deviations of Bp1 and Bp2 were measured to the nearest whole micron at 400X; each measurement for each basipodal segment is presented as the average of the measurements taken on the right and left P5.

In adult males, length measurements of individual segments of the left P5 were made according to procedures described by Frost (1971). Additionally, Re3 of the right P5 was measured from the proximal medial corner to the base of the medial terminal spine.

Data for the several types of measurements taken on the P5 of adult females and adult males are presented in a series of scatter diagrams with prosome length as the independent variable. Except in certain instances where comparisons of species are based on specimens taken from a single sample, an attempt was always made to represent the entire length range of each species in the various measurements. This simplifies interpretation of the measurements, since no unusually small or large specimens are likely to be found in the future which would significantly change my results. To clearly display the effect of body size on morphometric characters, specimens were selected so that their measurements would be approximately evenly distributed throughout the range of size of a species. All of the types of measurements of the P5 used here are correlated with prosome length and differences among the species are so obvious that they may be illustrated using simple linear regression analyses of the several measurements. Each regression coefficient obtained in these analyses was treated for significant deviation from zero. All of the measurements show increasing variance with increasing body size so that the usual comparison of regression lines by parametric statistical procedures are risky. Fortunately, in graphs representing two or more species there is always little doubt, in my opinion, whether a single regression line or multiple regression lines fit the data best.

Calanus finmarchicus Species Group

Species of the genus *Calanus* may be grouped in several ways (see, for example, Brodsky, 1967, 1972). One obvious group contains those species in which, as adults, a denticulate border is present on the medial margin of Bp1 of the P5. The species of this group may be further subdivided: (1) a single distinctive species *C. hyperboreus;* (2) a group containing *C. simillimus* and *C. propinquus;* (3) a complex of morphologically similar species — *C. finmarchicus, C. glacialis, C. helgolandicus, C. pacificus,* and three species more recently described by Brodsky (1959, 1965) as *C. australis, C. chilensis* and *C. sinicus*. This third group differs from the other two in a number of characters, most notably the lack of distinct points on the posterolateral margins of the TV in both sexes and reduced asymmetry of the P5 in the male. The species of the third group seem to represent two separate, albeit closely linked, evolutionary lineages. Accordingly, present-day representatives of these two lineages, including the new species described here, are placed in one of two species groups:

Calanus finmarchicus Species Group

C. finmarchicus (Gunnerus, 1765)
C. glacialis Jaschnov, 1955
C. marshallae n.sp.

Calanus helgolandicus Species Group

C. helgolandicus (Claus, 1863)
C. pacificus Brodsky, 1948
C. australis Brodsky, 1959
C. chilensis Brodsky, 1959
C. sinicus Brodsky, 1965

Distributional as well as morphological evidence may be cited in support of these groupings. Species of the *C. helgolandicus* group occur in mid-latitude, temperate regions of both hemispheres (e.g. Brodsky, 1965; Matthews, 1969; Jaschnov, 1970) while the *C. finmarchicus* group is restricted, basically, to polar and boreal waters of the Northern Hemisphere (Jaschnov, 1970). In adult females of the *C. helgolandicus* group the forehead is more angular, both in lateral and dorsal views, than that of females in the *C. finmarchicus* group (see Sars, 1901, Plates I and III; Brodsky, 1950, Figs. 19 and 20; Jaschnov, 1957a, Figs. 1 and 2). The forehead of *C. sinicus* most closely approaches that of females of the *C. finmarchicus* group but

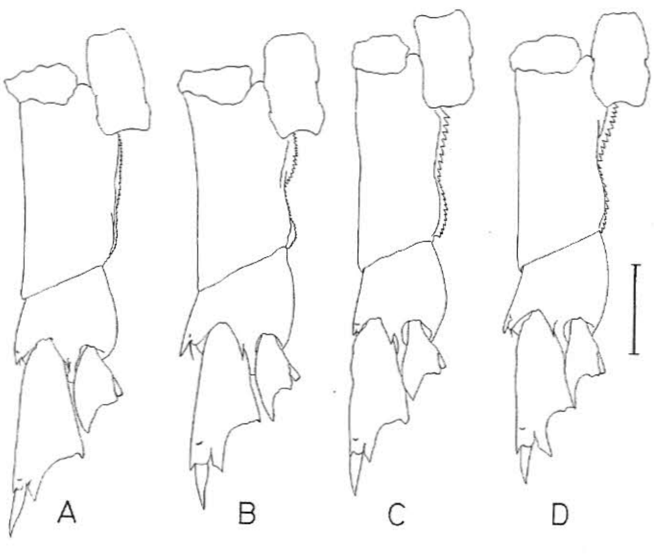

Fig. 6. *Calanus*. Basipod, Re1 and Ri1 of P5 (anterior view) illustrating differences between members of *C. finmarchicus* and *C. helgolandicus* species groups. Right P5 for (A) female *C. finmarchicus,* (B) female *C. helgolandicus,* (C) male *C. finmarchicus,* (D) male *C. helgolandicus*

is nevertheless slightly but distinctively angular, although this is not clearly illustrated by Brodsky (1965). Adults of both sexes in the *C. helgolandicus* group also differ from species of the *C. finmarchicus* group in certain structural aspects of the P5. To see these features, the appendage must be removed and examined in anterior view. In species of the *C. helgolandicus* group the outer distal corner of the Ri1 (both legs in female, right leg in male) extends nearly to or beyond the medial distal corner of the Re1; in adults of the *C. finmarchicus* group the outer distal corner of Re1 never extends close to the medial distal corner of the Re1 (Fig. 6). Further. species of the *C. helgolandicus* group bear, on the distal anterior margin of Bp2 of both right and left P4 and P5, an elongate, pointed, spiniform process; this process is shorter and pointed or blunt in species of the *C. finmarchicus* group (Fig. 6; see also Woodhouse, 1971). These characteristics were determined for the *C. helgolandicus* group from examination of adult specimens of the following species: *C. helgolandicus* (Raune Fjord, Norway; the English Channel off Plymouth, England; and the Mediterranean Sea near Barcelona, Spain), *C. pacificus* (Puget Sound, Washington; California Current; and the central North Pacific Ocean), *C. australis* (western South Atlantic Ocean), *C. australis* or *C. chilensis* (eastern South Pacific Ocean), and *C. sinicus* (central and western North Pacific Ocean).

Species Descriptions

Calanus finmarchicus and *C. glacialis*

Recent taxonomic study of these taxa and discussions concerning their status is reviewed by Frost (1971). Basically, differences of opinion about *Calanus finmarchicus* and *C. glacialis* revolve around the apparent lack of distinctive morphological characters separating the adult females. Jaschnov (1955, 1957a) distinguished *C. glacialis* and *C. finmarchicus* primarily on the basis of adult size and the structure of the P5, yet the two taxa appear to intergrade in some or all of the female characters used by Jaschnov (Grainger, 1961; Aurich, 1966; Matthews, 1966, 1967). Nevertheless, adult males of *C. finmarchicus* and *C. glacialis* can always be distinguished by the relative length of Re1 and Re2 of the left P5. When length measurements of either of these segments are plotted against prosome length, two non-overlapping clusters are obtained and variation of segment length within clusters is highly correlated with prosome length of the copepods (Frost, 1971, and below). Measurements of other segments of the male P5 vary continuously with prosome length over the combined range of size of *C. finmarchicus* and *C. glacialis* (Frost, 1971, and below) so that there is smooth intergradation between the species in these features. Most of the taxonomic characters previously utilized for adult females seem qualitatively to vary with size in the way just described; that is, they intergrade (see, for example, Grainger, 1961, Fig. 5). Analyses based heavily or entirely on these characters have led to the conclusion that *C. finmarchicus* and *C. glacialis* are either geographical variants of a single species (Aurich, 1966; Matthews, 1966, 1967; Brodsky, 1972) or two species which hybridize in rather narrow zones of geographical overlap (Jaschnov, 1972). The material used by Frost (1971) was collected from areas where *C. finmarchicus* and *C. glacialis* are allopatric as well as from regions of sympatry, and there is no indication from males in this material that the two taxa intergrade either where they co-occur or where they are allopatric. Frost (1971) infers from these observations, together with other data on distributions and life cycles, that *C. finmarchicus* and *C. glacialis* are distinct species and proposes that taxonomic characters previously employed for females are supraspecific (subgeneric) characters. Reanalysis of adult females generally supports this inference.

Adult Female. The analysis of adult females included detailed comparisons of body tagmata and all appendages with regard to both their morphology and mensural characteristics. From this study, a combination of basically 4 morphological features yield two distinguishable groups of females corresponding with *Calanus finmarchicus* and *C. glacialis*. These morphological features include (1) the outline, in lateral view, of the ventral surface of the genital segment posterior to the genital pore; (2) the shape of the posterolateral margins of TV; (3) a suite of characters, not all diagnostic, associated with the P5; (4) the proximity of the accessory photoreceptor and lateral gland of the forehead.

In *Calanus finmarchicus*, when viewed laterally, the ventral surface of the genital segment posterior to the genital pore is straight, or when it curves dorsad the curvature begins well posterior to the genital pore (Fig.4A). In *C. glacialis* the ventral surface curves continuously dorsad, beginning immediately at the genital pore and proceeding toward the posterior margin of the genital segment (Fig. 4B). The posterolateral margin of TV in *C. finmarchicus* is virtually always smoothly rounded, while that in *C. glacialis* is always either flattened or recurved just ventral (rarely dorsal) to the posterior-most point (Fig. 4A,B). The range of variation in these characters is presented in Figs. 4 and 7; often specimens must be examined under the compound microscope and care must be taken that the specimen is perfectly perpendicular to the observer. These two characters are used routinely to distinguish the two species; for example, in the large number of females (569 *C. finmarchicus*, 802 *C. glacialis*) represented in Fig. 12, all conformed with the descriptions above except 3 female *C. finmarchicus* in which the posterior margin of the TV was recurved. After specimens in my material were sorted into two groups on the basis of these features, other taxonomic characters were investigated.

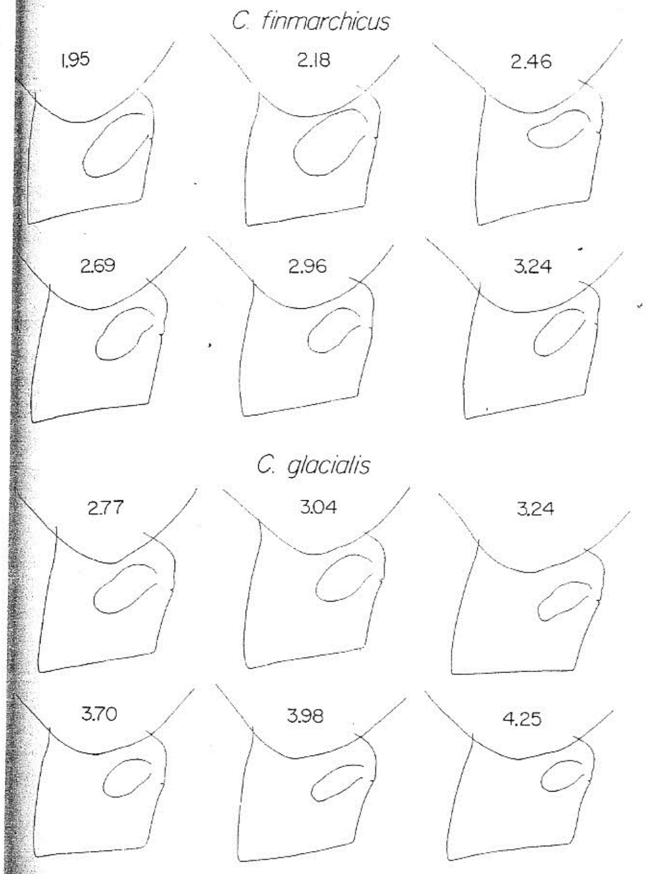

Fig. 7. *Calanus*. Posterolateral margin of TV and genital segment (right lateral view) for adult female *C. finmarchicus* (upper two rows) and *C. glacialis* (lower two rows). Virtually entire range of length of each species is represented (prosome lengths, in mm, are indicated). Illustrations were made at different magnifications to facilitate comparison

Jaschnov (1955, 1957a) emphasized the diagnostic difference between the two species in the curvature of the denticulate border on the medial margin of the Bpl of P5. In *Calanus finmarchicus* the denticulate border tends to be straight, while in *C. glacialis* it tends to be concave (Fig. 5). Kurich (1966), Matthews (1967), and later Jaschnov (1972) himself claimed intergradation between the species in this character, and Matthews and Jaschnov showed that the degree of curvature of the denticulate border varies with size. However, all of these authors appear to have drawn erroneous conclusions about the status of the species from these observations. This character was reexamined using two series of specimens. Series A consisted of 65 females each of *C. finmarchicus* and *C. glacialis*, selected to represent nearly the entire range of size of both species and their geographical ranges. Series B contained 50 females of each species selected from a plankton sample collected in the Greenland Sea (67°12'N; 25°34'W, 5 May, 1965); this additional series from a single sample was chosen because both Matthews and Jaschnov employed single plankton samples to study the character. After the specimens in each series had been identified to species by the shape of the genital segment and posterolateral margin of the TV, curvature of the denticulate margin of Bpl was measured as described earlier (see Fig. 5). The results (Fig. 8, upper graphs) confirm that the deviation of Bpl may vary directly with size of the female and that the species overlap somewhat in this character, but in both series the species form two definite clusters (indicated by vertically separated, nearly parallel regression lines) and clearly do not intergrade continuously. The two series differ somewhat in the relationship between prosome length and the magnitude of the deviation of Bpl. The two least-squares regression lines fitted to data for Series A both had slopes differing significantly from zero, clearly indicating a correlation between size of female and deviation of Bpl. In Series B, neither regression line had a slope differing significantly from zero. However, because of the great variability in this measurement and since the entire length range of neither species is represented in this series, the disagreement between the two series is very likely due to this. When the data for each species in the two series are combined, the regression lines fitted to each set of data have slopes differing significantly from zero (see Fig. 19A).

Except for the reduced vertical displacement, the distribution of deviation measurements in Fig. 8 (upper graphs) resembles that for length measurements of Re1 and Re2 of the male left P5 (Fig. 13A, B). However, unlike the latter measurements, deviation of Bpl is not a diagnostic character, because measurements for the two species overlap slightly. Therefore, as suggested by Frost (1971), deviation of Bpl must be viewed as a supraspecific taxonomic character much like, for example, length of Re3 of the male right P5 (Fig. 13C). Nevertheless, since in Fig. 8 there is no smooth intergradation between the species, the data do not support the claim that *Calanus finmarchicus* and *C. glacialis* comprise a single variable species (Matthews, 1967). Nor is it necessary to conclude from Fig. 8 that *C. finmarchicus* and *C. glacialis* hybridize where they co-occur (Jaschnov, 1972). Rather, the spread of points about each regression line in both graphs is approximately uniform throughout the range of length of both species, indicating that nothing unusual is happening to the character in specimens of the two species which are about the same size. Jaschnov's measurements (1972, Fig. 3), although somewhat more variable, are not at odds with my data; but I cannot explain why Matthews' illustration (1967, Fig. 4), based on many more measurements, differs substantially from mine and Jaschnov's. It should, however, be again noted that Matthews' measurements of deviation are too large by a factor of 10 (Jaschnov, 1972) and there may be other systematic errors in his measurements. Also, Matthews' (1966) exper-

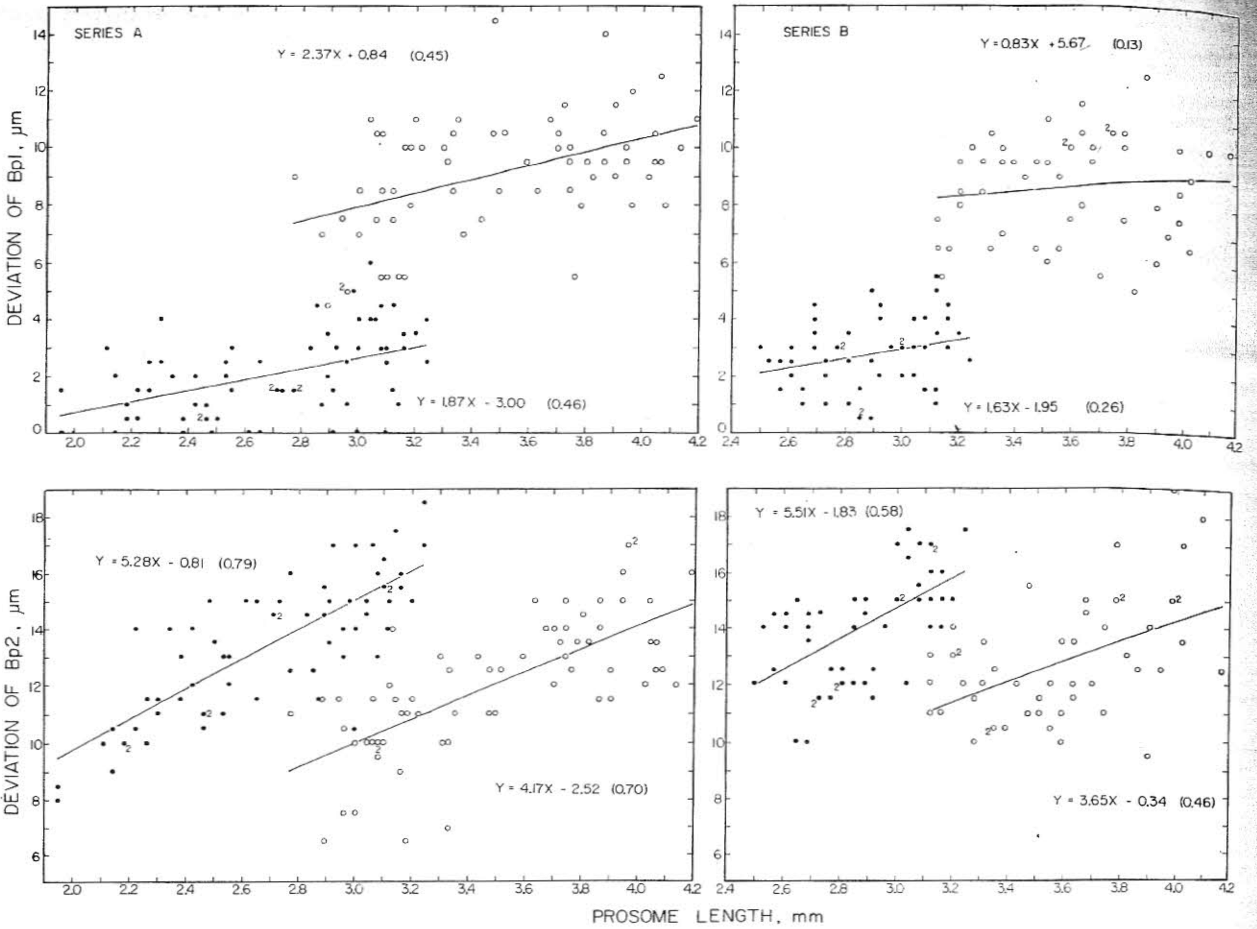

Fig. 8. *Calanus*. Upper graphs: curvature (deviation) of medial margin of Bp1 of female P5 plotted against prosome length (solid dots, *C. finmarchicus;* open circles, *C. glacialis;* "2" indicates more than one observation for coordinates); equations of least-squares regression lines and correlation coefficients (parentheses) are given; slopes of the two regression lines for Series A differ significantly from zero ($P < 0.001$ for both), those for Series B do not (*C. finmarchicus*, $0.1 > P > 0.05$; *C. glacialis*, $P \sim 0.4$). Lower graphs: curvature (deviation) of medial margin of Bp2 of female P5 plotted against prosome length. All 4 regression lines have slopes differing significantly from zero ($P < 0.001$ for all 4 lines)

imental studies of this character in *C. finmarchicus* agree with our results and, contrary to his later conclusions from this work (Matthews, 1967), do not necessarily indicate that *C. finmarchicus* and *C. glacialis* do not separate into two groups. Since Matthews (1966) cultured larger specimens of *C. finmarchicus* at lower experimental temperatures, then it follows that deviation of Bp1 of P5 in his specimens should be inversely related to temperature because, as shown above, deviation varies directly with the size of the animal.

Calanus finmarchicus and *C. glacialis* also form two definite clusters, with some overlap, when the number of denticles on the medial margin of Bp1 of P5 is plotted against prosome length. My plot (not shown, but see Table 1) is quite similar to that of Matthews (1967, Fig. 8a), showing that within the species the number of denticles is directly correlated with the size of the animal and that the two species do not intergrade smoothly in this character, either. When all length classes of each species are evenly represented, the average number of denticles differs for the two species (Table 1).

Apparently unnoticed by previous workers is th difference between *Calanus finmarchicus* and *C. glacialis* in the degree of curvature of the media margin of Bp2 of P5. The medial margin tends to b strongly convex in *C. finmarchicus* and much less convex in *C. glacialis* (Fig. 5). To quantify this pattern, the curvature of the medial margin of Bp was measured as described earlier (see Fig. 5). The pattern of measurements (Fig. 8, lower graphs is similar to that for Bp1, in that the deviation of Bp2 varies directly with size and there is som overlap between the species but, again, the speci

Table 1. *Calanus finmarchicus* species group. Number of denticles on denticulate medial margin of Bp1 of P5 in adult females. All length classes of each species are approximately evenly represented. Counts of both basipods of each specimen were averaged. m: Mean number of denticles for each species; se: standard error; n: number of specimens examined; -: no specimens with that number of denticles

Calanus species	Number of denticles																m	se	n
	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48			
C. finmarchicus	1	-	-	2	1	8	13	17	25	27	15	16	8	3	1	2	34.71	0.40	139
C. glacialis	-	-	-	5	21	19	25	23	25	8	1	2	1	-	1	-	30.20	0.34	131
C. marshallae	1	5	8	11	17	16	13	7	2	1	-	-	-	-	-	-	26.15	0.43	81

form definite clusters and do not intergrade continuously in this character. In sum, although curvature of the medial margins of the two basipodal segments of the P5, taken separately, are not diagnostic characters. they certainly provide evidence that two statistically different populations were sampled and in no way contradict my belief that *C. finmarchicus* and *C. glacialis* are distinct species.

Since the curvatures of Bp1 and Bp2 tend in opposite directions in the two species, a combination of the measurements of deviation is diagnostic, at least for the 230 females used in the above analysis. The diagnostic character, called P5 index, is obtained by taking the numerical difference of the deviations of Bp1 and Bp2:

P5 index = (Deviation of Bp2 - Deviation of Bp1).

While it was observed above that the two species overlap somewhat in the separate measurements of deviation, they form discrete clusters based on the P5 index (Fig. 9). However, because of the great variability in the index, there is a significant chance that a specimen of one species will be found whose P5 index falls into the cluster represented by the other species.

Other, more subtle features are useful for differentiating females of *Calanus finmarchicus* and *C. glacialis*. In *C. finmarchicus*, the spiniform process on the distal anterior margin of Bp2 of the P5 is nearly always thin and sharply pointed while the outer distal corner of Ri1 is broadly tapered, usually blunt. By contrast, in *C. glacialis*, the spiniform process on the distal anterior margin of Bp2 is usually thick and blunt on at least one leg and the outer distal corner of Ri1 is narrowly tapered and sharply pointed (Figs. 5, 10). The accessory photoreceptor and lateral gland of the forehead in *C. finmarchicus* are usually located very close to one another, while in *C. glacialis* the accessory photoreceptor is well anteriad of the lateral gland (Fig. 2A,B).

Williams (1972) suggested that *Calanus finmarchicus* and *C. glacialis* could be distinguished by the shape and orientation of the seminal receptacle (spermatheca) within the genital segment. I disagree, for I found extensive overlap between the two species in this feature. Williams probably was misled by making comparisons only of small specimens of *C. finmarchicus* and large specimens of *C. glacialis*; in fact, the differences described by Williams are not apparent in like-sized specimens of the two species (Fig. 11).

The range of size of *Calanus glacialis* illustrated in Fig. 9 is surprising in view of the length measurements for this species given by Jaschnov (1972) and others. In regions where *C. finmarchicus* and *C. glacialis* co-occur, they overlap in size to a much greater extent than hitherto demonstrated. To show this, length-frequency histograms were constructed for three series of females from plankton samples collected in three widely separated areas of sympatry: Gulf of Maine, Greenland Sea, and Barents Sea. For comparison, length-frequency histograms were also constructed for an allopatric population of *C. finmarchicus* in the western North Atlantic Ocean and an allopatric population of *C. glacialis* in the central Arctic Ocean (cf. Jaschnov, 1970, Figs. 1 and 2). The length-frequency curves of sympatric populations are rather similar for all three regions (Fig. 12), and yield the statistics on length of the species given in Table 2. The size range of *C. finmarchicus* in these samples is similar to that found by others but, unexpectedly, the lower limit of length for *C. glacialis* is about 0.4 mm less than the shortest length given for this species in the literature. For each species the variation in pro-