

SOME ASPECTS OF THE BIOLOGY OF
PARATHEMISTO (AMPHIPODA: HYPERIIDEA)
FROM THE GULF OF ST. LAWRENCE

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ABSTRACT

The distribution, life history and systematics of Parathemisto gaudichaudi (forms bispinosa and compressa) and Parathemisto abyssorum in the Gulf of St. Lawrence were investigated, using material collected between May and September of 1969. P. abyssorum is the dominant pelagic amphipod inside the Gulf. The highest concentration of this species and of both forms of P. gaudichaudi is in the central and eastern Gulf; their distribution is largely dependent on the current system. P. abyssorum appears to show a one-year life cycle in which the adults die after spawning in the spring. P. gaudichaudi also spawns largely in the spring but it is not certain whether these adults also die after liberating their young. The morphology of form bispinosa, form compressa and P. abyssorum was examined, and it is possible that the differences between bispinosa and compressa are significant enough to warrant their separation as species.

SHORT TITLE: The pelagic amphipods of the Gulf of St. Lawrence.

SOME ASPECTS OF THE BIOLOGY OF PARATHEMISTO
(AMPHIPODA: HYPERIIDEA) FROM THE GULF OF ST. LAWRENCE

by

Susan A. Hoffer

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I. GENERAL INTRODUCTION

a. The Project.

A series of cruises, organized for the purpose of examining production in the Gulf of St. Lawrence, was initiated by the Canadian Committee of the International Biological Programme, directed by Dr. D.M. Steven. Collections made between the months of May and September in 1969 have provided the material that was used in this investigation.

The zooplankton community serves as the important link between primary and fish production and among its conspicuous members in the Gulf are the calanoid and cyclopoid copepods, the euphausiids and the hyperiid amphipods. Of the latter, most or all of which are voracious carnivores and of considerable significance in the economy of the Gulf, the genus Parathemisto constitutes the largest proportion, and the distribution of its various species is examined here. Growth and life cycles are also described within the limitations of the samples.

The systematics of the genus Parathemisto have been in a state of confusion since its initial discovery and description by Guérin in 1825. Causing most of the trouble is the species gaudichaudi with its two forms compressa and bispinosa, and this problem is considered in the final sections of this study.

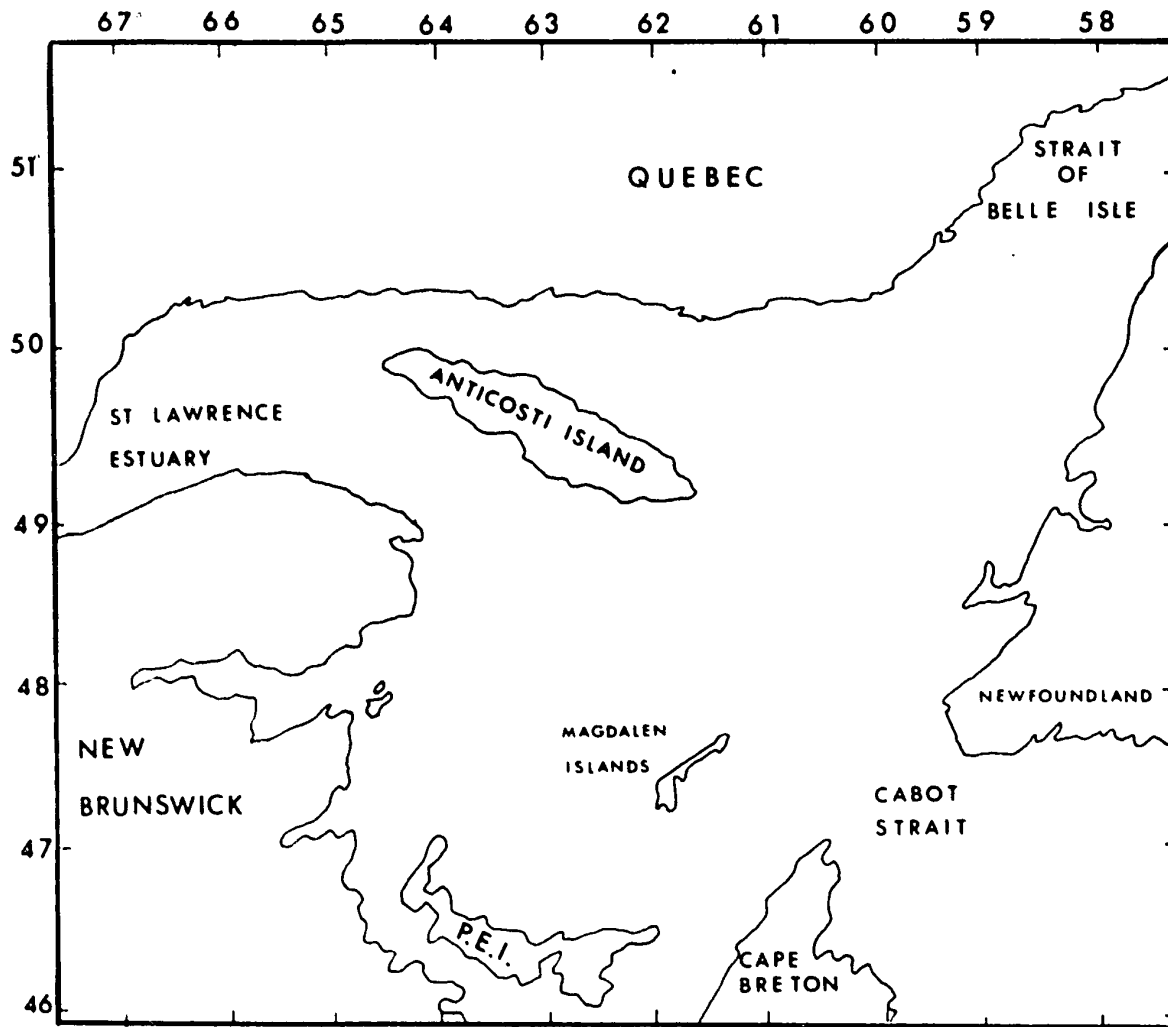
b. The Study Area

Between latitudes 46°N and 52°N lies the shallow inland sea of the Gulf of St. Lawrence, a body of water occupying an area of 214×10^3 sq km (Forrester and Vandall, 1968). The Gulf is shown in Figure 1.

Stretching from the edge of the Continental Shelf to the mouth of the Saguenay River is the Laurentian Channel which, along with its branch, the Esquiman Channel, forms a conspicuous feature of the Gulf. Also important is the establishment during the late spring and summer months of a three-layer system of water masses consisting of a warm surface layer extending to a depth of about 40 m, an intermediate cold layer from about 40 to 225 m, and a deep warm layer from 225 m to the bottom (Forrester, 1964). During the winter, the two upper layers mix and form a single cold layer which then overlies the permanent warm layer at the bottom. Forrester (1964) calculated the mean summer temperatures to be 9.2°C for the surface layer, 1.4°C for the intermediate layer, and 4.6°C for the deep layer.

The principal connections of the Gulf with the Atlantic Ocean are Cabot Strait and the Strait of Belle Isle. Through the latter there is an intermittent inflow of Labrador Current water and an outflow of Gulf water along the Newfoundland coast. The net transport, however, is negligible (Huntsman, Bailey and Hachey, 1954). Cabot Strait is the main door to the open ocean. Its circulation is characterized by a weak inward surface flow of water on the Newfoundland side and a strong outward surface flow on the Cape Breton side (McGregor, 1956). The net flow is outward as would be expected due to the

Figure 1. The Gulf of St. Lawrence.



progressive drainage into the Gulf from the St. Lawrence and other small rivers.

II. MATERIALS AND METHODS

a. Sampling.

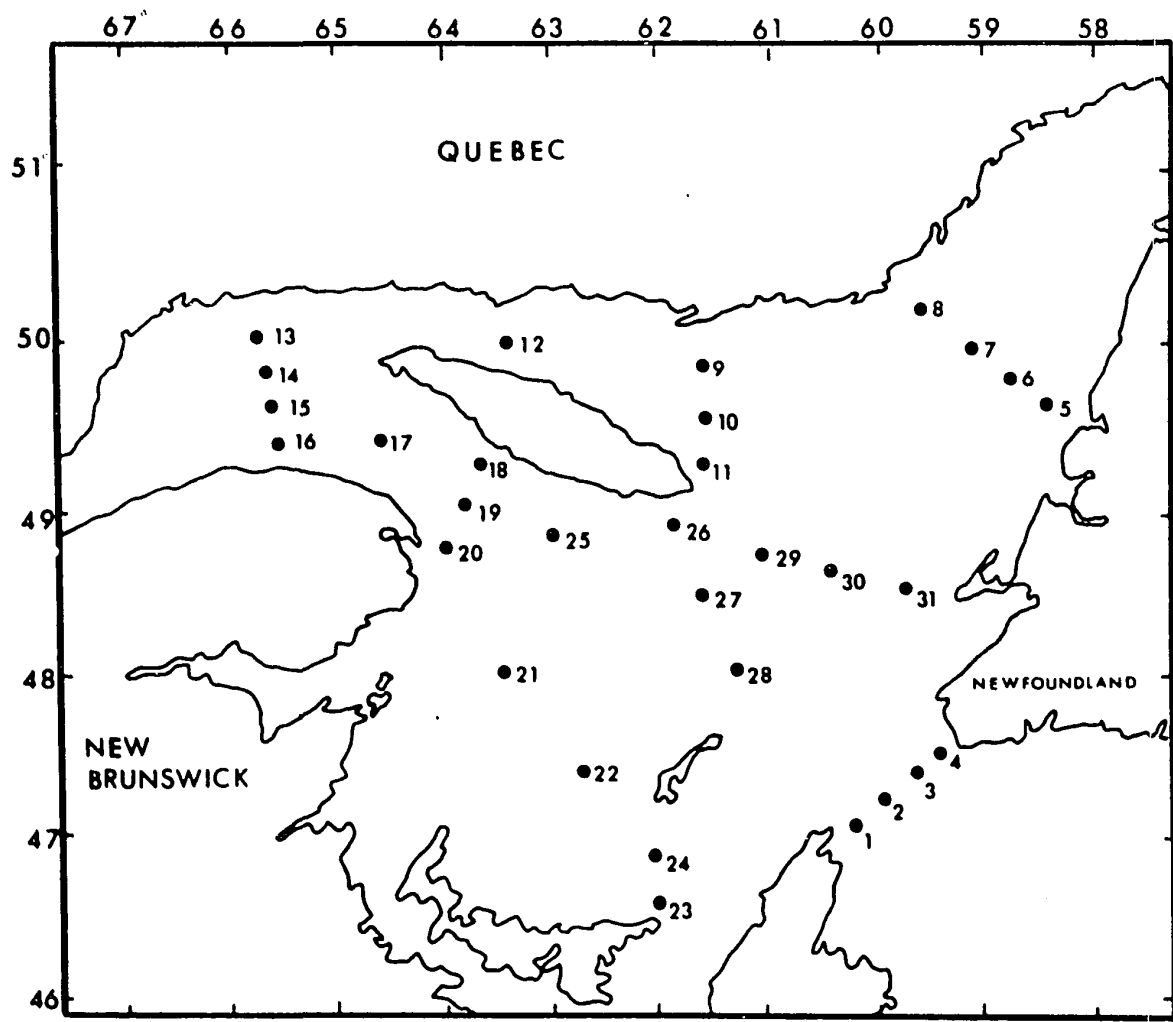
The material for this study was collected during the late spring and summer of 1969 on the cruises of the "Ambrose Foote", chartered by the Gulf of St. Lawrence project of the International Biological Programme. Altogether there were 31 stations in the Gulf, the locations of which are given in Appendix I. The stations are also shown in Figure 2. Collections were made between May 7 and September 24 - excluding a short eighth cruise which was held after that date and is not considered in this study. Not every station was visited on each cruise and alternations were made between 21-24, 25-28, and 25-26 together with 29-31. Appendix II lists the schedule with the dates of each cruise and the stations sampled, and Appendix III gives the depths of each oblique sample.

Oblique and horizontal tows were taken at each station using 1/2 meter nylon nets of mesh sizes 0, 6 and 20. Closing nets were used for the horizontal tows. Collections were generally between 10 and 20 minutes duration and flowmeters were attached to record the volume of water filtered by the net. A Time Depth Recorder provided information on the depths sampled by each tow, and a Bathythermograph supplied a continuous temperature-depth reading.

b. Treatment of the Samples.

The material for this study was taken from the oblique no. 0 samples except in a very few cases in which it was not available.

Figure 2. The stations.



In these instances the no. 6 sample was substituted. The composition of pelagic amphipods proved very similar from both nets. The horizontal tows from stations 5-8 were briefly examined as well, but the information for both the life cycles and horizontal distributions was gathered only from the oblique tows. The material had previously been subsampled, leaving a 3/4 or 1/2 sample to be examined. Occasionally, when the number of amphipods was unusually high, it was again subsampled by the author. All the figures quoted in this paper pertaining to P. abyssorum (Boeck) and P. gaudichaudi (Guérin) are corrected to represent complete samples.

All the animals were counted, sexed and measured. Measurements were to the nearest tenth of a millimeter along the dorsal line from the head to the tip of the third pair of uropods. Mature females were distinguished by the presence of brood lamellae as large as, or larger than, the gill plates. There was only a small number of males, and their maturity was ascertained by the development of the long antennae.

Modal lengths were used in the calculation of growth rates. For the determination of horizontal distributions, the number of animals was corrected to individuals per 100 cu m.

The gut content analysis was carried out on animals collected in the Gulf, but the information concerning the feeding habits of Parathemisto abyssorum was gained from experimental work at the Logy Bay Marine Station in St. John's, Newfoundland. The animals were collected with a no. 0 net and maintained in the laboratory which was

equipped with running sea water.

P. gaudichaudi is comprised of two forms, form bispinosa and form compressa. Foremost among the characters by which bispinosa, compressa and P. abyssorum are taxonomically separated are the length of the fifth peraeopod (P5) relative to the sixth and seventh (P6, P7), and the shape of the fifth joint of peraeopods 3 and 4 (P3, P4). Peraeopods 5, 6 and 7 of P. abyssorum are approximately equal in length and the margins of joint 5 of P3 and P4 are almost parallel. On the other hand, in both forms of P. gaudichaudi, the length of P5 is distinctly greater than that of P6 and P7, and the margins of the fifth joint of P3 and P4 are expanded. Forms bispinosa and compressa differ a great deal in the length of P5 -- that of the former being much greater -- and in the degree to which the margins of the fifth joint on P3 and P4 depart from parallelism -- those of bispinosa being further expanded.

Consequently, the following ratios were measured, both for females over 8 mm and for individuals between 4 and 7 mm:

- 1) The length ratio of the fifth joint of P5 to the fifth joint of P6.
- 2) The length ratio of the sixth joint of P5 to the sixth joint of P6.
- 3) The length ratio of the fifth joint of P5 to the body (as measured from the head to the tip of the uropods).

4) The length/width ratio of the fifth joint of P4.

Frequency distributions were then prepared, each distribution based on the measurements of 50 individuals, and the statistic which was applied to them involves the determination of the degree of intergradation, or convergence, between forms. It is expressed as the average percentage of the area of overlap relative to the entire curve for each of the two forms whose affinities are being examined (Ginsberg, 1938). For example, if 14% of compressa and 6% of P. abyssorum were in the area of overlap, then the degree of convergence between them would be 10%. In the case of one pair of frequency distributions (see bispinosa and compressa, Figure 17), an intergradation value could not be calculated. A t-test was applied to the means of the distributions in question and to another pair of distributions (see compressa and P. abyssorum, Figure 17) and from the results the intergradation value was estimated (see Table 8).

III. RESULTS

PART A. SYNOPSIS OF THE HYPERIIDS COLLECTED

a. Parathemisto libellula (Lichtenstein)syn. Themisto libellula (Mandt)

Only three immature specimens were obtained from the samples which I examined, and each of these was taken from station 8, in waters influenced by the Labrador Current. One individual was recorded from a depth of 90-100 m on June 6 about 9:30 am and the remaining two on June 25 at approximately 9:45 am from a depth of 100 m. Dunbar (1954) describes Parathemisto libellula as both an arctic and subarctic species, but more dominant in the former. In Folio 6 of the "Serial Atlas of the Marine Environment" (1964), Dunbar cites the Strait of Belle Isle as its southernmost limit. The specimens I have examined probably represent a few "stragglers" of that portion of the population carried into the Strait in the cold Labrador Current. The species appears to be absent in the Gulf proper, an observation confirming the findings of Huntsman (unpublished MS quoted in Bousfield, 1951).

The animals that were found were recorded early in the morning in the deeper water of the Strait of Belle Isle. Both Bousfield (1951) and Dunbar (1946), however, have located Parathemisto libellula in surface water during the day. Furthermore, Dunbar (1946) also found evidence to suggest that as the light becomes stronger in late spring and summer, the species is found increasingly close to the surface. Since it was not

collected after June, it is probable that the surface waters had become too warm by that time.

b. Hyperorche medusarum (Krøyer)

Altogether, eight specimens of Hyperorche medusarum were collected from stations across the Strait of Belle Isle. Taken from shallow horizontal tows were three immature individuals, one of which was from a depth of 19 m at station 8 about 7:30 pm on June 5, and two of which were from a depth of 25 m at station 5 on August 21 about 9:30 am. These few observations are in agreement with Bousfield (1951), who has stated that Hyperorche medusarum is generally found near the surface. Of five individuals collected in oblique tows, one mature male and one mature female were taken from station 8 on June 25 and three immature specimens were recorded from station 5, one on July 17 and two on August 2.

Dunbar (1954) describes this species as arctic, subarctic and boreal. Stephensen (1942) found it largely between 50°N and 70°N in the Atlantic, although it may penetrate as far south as the Gulf of Maine (Bigelow, 1926). Although I failed to find Hyperorche medusarum within the Gulf proper, Shoemaker (1930), in his examination of the material from the 1917 Cheticamp Expedition, did report its presence in the southwestern part of the Gulf.

c. Hyperia galba (Montague)

One mature female was collected by an oblique tow at station 2 on July 7. Predominantly subarctic, but arctic as well (Dunbar,

1954), Hyperia galba was reported by Bigelow (1926) to be present but scarce in the Gulf of Maine. It has also been reported by Huntsman (unpublished MS quoted in Bousfield, 1951) off the outer coast of Nova Scotia and within the Gulf of St. Lawrence.

d. Parathemisto gaudichaudi (Guérin)
form compressa (Goës)

A total of 1182 specimens of compressa larger than 4 mm were taken from the oblique tows examined. Although this form is present throughout most of the Gulf, it is particularly abundant in the central and eastern sections, but notably rare in the areas of the St. Lawrence Estuary and the Magdalen Shallows. The distribution of this hyperiid as well as that of bispinosa and Parathemisto abyssorum will be discussed in greater detail in another section.

e. Parathemisto gaudichaudi (Guérin)
form bispinosa (Boeck)

Altogether, 205 individuals over 4 mm were collected from the oblique tows. Like the compressa form, it is very rare at stations 13 through 24. It is relatively abundant in the southeastern part of the Gulf.

Individuals under 4 mm, of which there were 755, were identified only as gaudichaudi and not specified to bispinosa or compressa.

f. Parathemisto abyssorum (Boeck)

syn. Parathemisto oblivia (Krøyer)

This species is by far the most abundant hyperiid in the Gulf. Approximately 4000 individuals, representing all stages, were taken by the oblique no. 0 tows, as compared with a total of only 2142 specimens of both forms and all stages of Parathemisto gaudichaudi. Furthermore, this species is well represented in all parts of the Gulf except the Magdalen Shallows.

PART B. DISTRIBUTION

Parathemisto gaudichaudi is a conspicuous constituent of the plankton, occurring frequently in the colder waters of both hemispheres (Kane, 1966). In the northern hemisphere, Dunbar (1964) describes this species as generally subarctic. Sars (1895) found it both in Davis Strait and in the waters off Spitzbergen and East Greenland, and Stephensen (1933 and 1940) reported it in Davis Strait and in shallow Icelandic waters. P. gaudichaudi has also been described from Ungava Bay (Dunbar, 1954), Hudson Strait (Dunbar, 1964) and northern Foxe Basin (Grainger, 1962). At lower latitudes, Pinhey (1927), Shoemaker (1930) and Bousfield (1951) have reported P. gaudichaudi in the Gulf of St. Lawrence and in the offshore waters of Newfoundland. Bigelow (1926) has described it as the most widely distributed hyperiid in the offshore waters of the Gulf of Maine. On the European side of the Atlantic, it has been described from Iceland, the British Isles, Greenland and the Bay of Biscay (Stephensen, 1923, 1924, 1942). Tattersall (1906) has reported this species off

the coast of Ireland, and Le Danois (1921) gives records of it off the coast of France. In the southern Atlantic, it is present in both the Antarctic and Subantarctic (Kane, 1966).

Although the distributions of bispinosa and compressa are approximately parallel (Stephensen, 1924; Bousfield, 1951; others), a number of differences in their niches have been reported. Bigelow (1926) observed in the Gulf of Maine that bispinosa is generally found in deeper waters than compressa and is the more oceanic of the two, having been taken more frequently in deep offshore hauls. Barnard (1932) also found that bispinosa is more numerous in the open ocean of the southern hemisphere and Tesch (1911) has reported that it is the more oceanic on the eastern side of the Atlantic as well. Finally, Barnard (1932) and Kane (1966) have both found that bispinosa tends to inhabit slightly higher latitudes than compressa. From 33°S to 72°S in the Southern Atlantic, the proportion of bispinosa increases from 9% to 75% (Kane, 1966).

Parathemisto abyssorum is present throughout both arctic and subarctic waters (Dunbar, 1954) and Schellenberg (1927) reported it as far south as 45°N. It is apparently absent in the Southern Atlantic however (Kane, 1966). It was collected by Barnard (1959) from vertical tows in the upper 200 m of the Central Arctic Basin, by Stephensen (1923 and 1942) off Spitzbergen, in the waters off Greenland and in the Barents Sea and by Grainger (1962, 1965) in Foxe Basin, Amundsen Gulf and M'Clure Strait. Dunbar (1954, 1964)

has found this species in Ungava Bay, Baffin Bay and Disco Bay as well as in Hudson Strait, northern Hudson Bay and off the Labrador coast. Shen (1966) provides additional records in the Northwest Atlantic. Further south, Pinhey (1927), Shoemaker (1930) and Bousfield (1951) have described P. abyssorum from the Gulf of St. Lawrence, and Bigelow (1926) has recorded its presence in minor quantities from the Gulf of Maine. According to the same worker, P. abyssorum is more abundant in the Northeast Atlantic and Stephensen (1929, 1942) has reported it in the Norwegian Sea and in the waters around Iceland and Greenland.

Although at higher latitudes this species is encountered in both deep and shallow water (Dunbar, 1964), at lower latitudes it is normally found in deep water (Bousfield, 1951).

a. The Distribution of Parathemisto abyssorum in the Gulf of St. Lawrence.

Of the various hyperiids found in the Gulf, P. abyssorum is not only the most abundant, it is also the most widely distributed. There is, however, a zone of maximum concentration south of Anticosti Island and to the northeast of it. This is apparent both in Figures 3 and 4 and in Table 1, all of which represent distributions averaged over the seven cruises for each station. Organisms larger than 4 mm are equally distributed across Cabot Strait, but in the Strait of Belle Isle, where they are more abundant, there is a greater number at the two deeper stations, namely 6 and 7. The smaller individuals are

Figure 3. Parathemisto abyssorum. The distribution of individuals greater than or equal to 4.1 mm. The quantities represent the catch converted to numbers per 100 cu m and averaged during the period covered by the seven cruises.

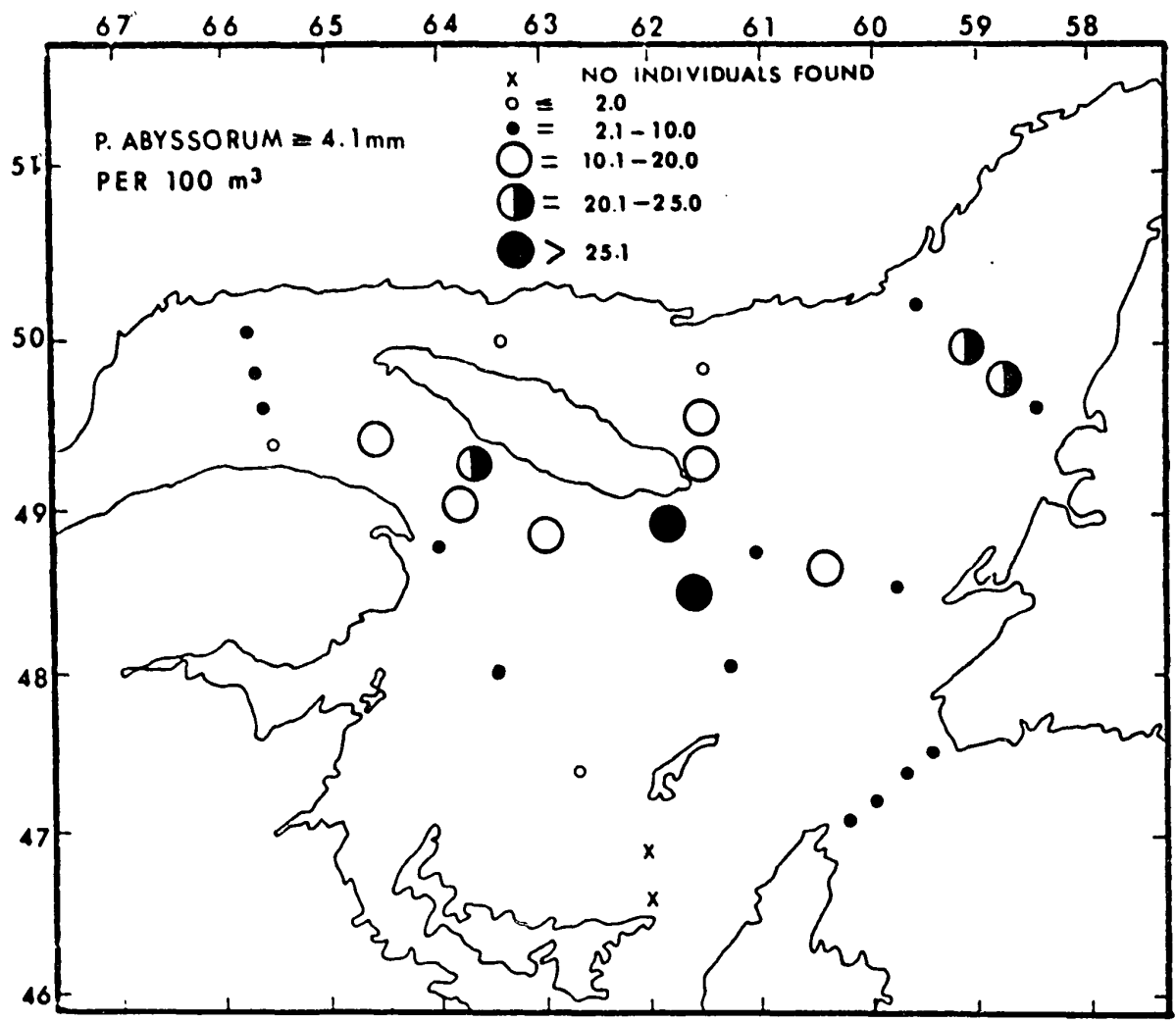


Figure 4. Parathemisto abyssorum. The averaged distribution per 100 cu m of individuals less than or equal to 4.0 mm. See Figure 3 for code.

Table 1. The distribution of P. abyssorum in the Gulf of St. Lawrence. Their numbers have been corrected to represent complete samples per 100 cu m and averaged.

Station	Number <u>P. abyssorum</u> greater than or equal to 4.1 mm	Number <u>P. abyssorum</u> less than or equal to 4.0 mm
1	2.565	1.826
2	5.728	11.451
3	4.785	94.102
4	8.475	.572
5	4.035	1.006
6	11.550	.754
7	21.554	1.440
8	8.357	.359
9	1.464	.406
10	17.778	10.196
11	11.790	134.571
12	2.053	4.048
13	4.893	3.944
14	8.228	2.410
15	2.233	.713
16	1.197	.259
17	10.728	1.305
18	22.147	4.475
19	11.725	.169
20	2.778	6.878
21	3.983	0
22	.417	1.667
23	0	0
24	0	0
25	11.717	1.923
26	77.339	22.229
27	61.779	7.453
28	8.217	22.252
29	7.696	0
30	13.105	1.429
31	6.076	2.604

similarly distributed, except that they occur in Cabot Strait in larger numbers than in the Strait of Belle Isle.

The organism is concentrated for the most part in the deeper parts of the Gulf (notably stations 18, 26 and 27) and is conspicuously rare in the Magdalen Shallows.

The majority, both adults and juveniles, were collected inside the Gulf of St. Lawrence proper rather than in the straits. This indicates the existence of a local self-sustaining population, although their presence in both Cabot Strait and in the Strait of Belle Isle shows that both entrances do act as a source of recruitment to some extent. Bousfield (1951) has shown that P. abyssorum is widely distributed and is indeed the dominant pelagic amphipod in the Strait of Belle Isle, hypothesizing that this cold water species succeeds in breeding in the Gulf of St. Lawrence by exploiting the intermediate cold layer that exists throughout the year. Figure 4 shows that this species does in fact breed successfully inside the Gulf, although relatively few juveniles were collected from stations 5-8. Appendices IV and V give the cruise by cruise distributions of P. abyssorum respectively greater than, and less than, 4 mm. The peak abundance of this species occurs in the spring and coincides thus with the period of maximum spawning.

b. The Distribution of Parathemisto gaudichaudi in the
Gulf of St. Lawrence

In this section only, unless otherwise stated, the terms bispinosa and compressa refer to individuals larger than 4 mm, whereas

the term P. gaudichaudi refers to those specimens of both forms under this length. The numbers of individuals of compressa, bispinosa and P. gaudichaudi that were collected on each cruise are given in Appendices VI, VII, and VIII respectively and Figures 5, 6, and 7 illustrate the collections averaged over the entire period, with the exact figures shown in Table 2.

As in the case of P. abyssorum, there seems to be a local resident population concentrated in the central and eastern Gulf with most of the breeding in these same areas. This applies largely to compressa, for bispinosa does not appear to be very successful in the Gulf of St. Lawrence. Only 316 of the latter were collected, compared with 1039 of the former. As with P. abyssorum, both forms are rare in the Magdalen Shallows. Both also reach a peak abundance during the spring spawning period.

c. Relations to Currents.

Neither the distribution of P. abyssorum nor that of P. gaudichaudi (all stages) is correlated with the areas of maximum primary production in the Gulf which is in the northwest section (Steven, 1971). Instead, the distributions appear to depend on the surface current system in the straits and inside the Gulf. I have said that both P. abyssorum and P. gaudichaudi are concentrated in the central and eastern sections of the Gulf surrounding Anticosti Island. This area coincides approximately with the central gyre of the Gulf into which feed the surface currents from both Cabot Strait

Figure 5. Parathemisto gaudichaudi, form compressa. The averaged distribution per 100 cu m of individuals greater than or equal to 4.1 mm. See Figure 3 for the code.

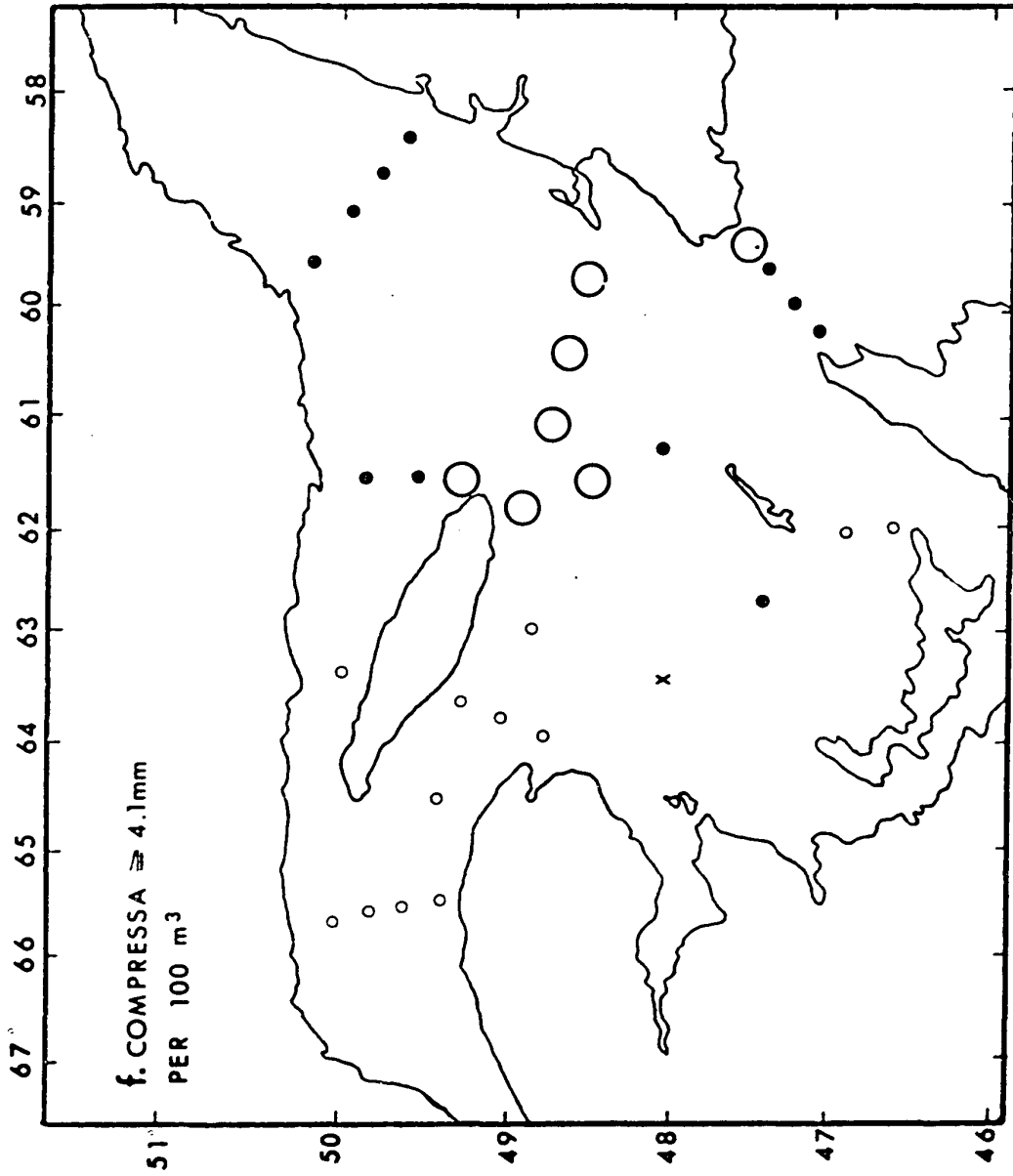


Figure 6. Parathemisto gaudichaudi, form bispinosa. The averaged distribution per 100 cu m of individuals greater than or equal to 4.1 mm. See Figure 3 for the code.

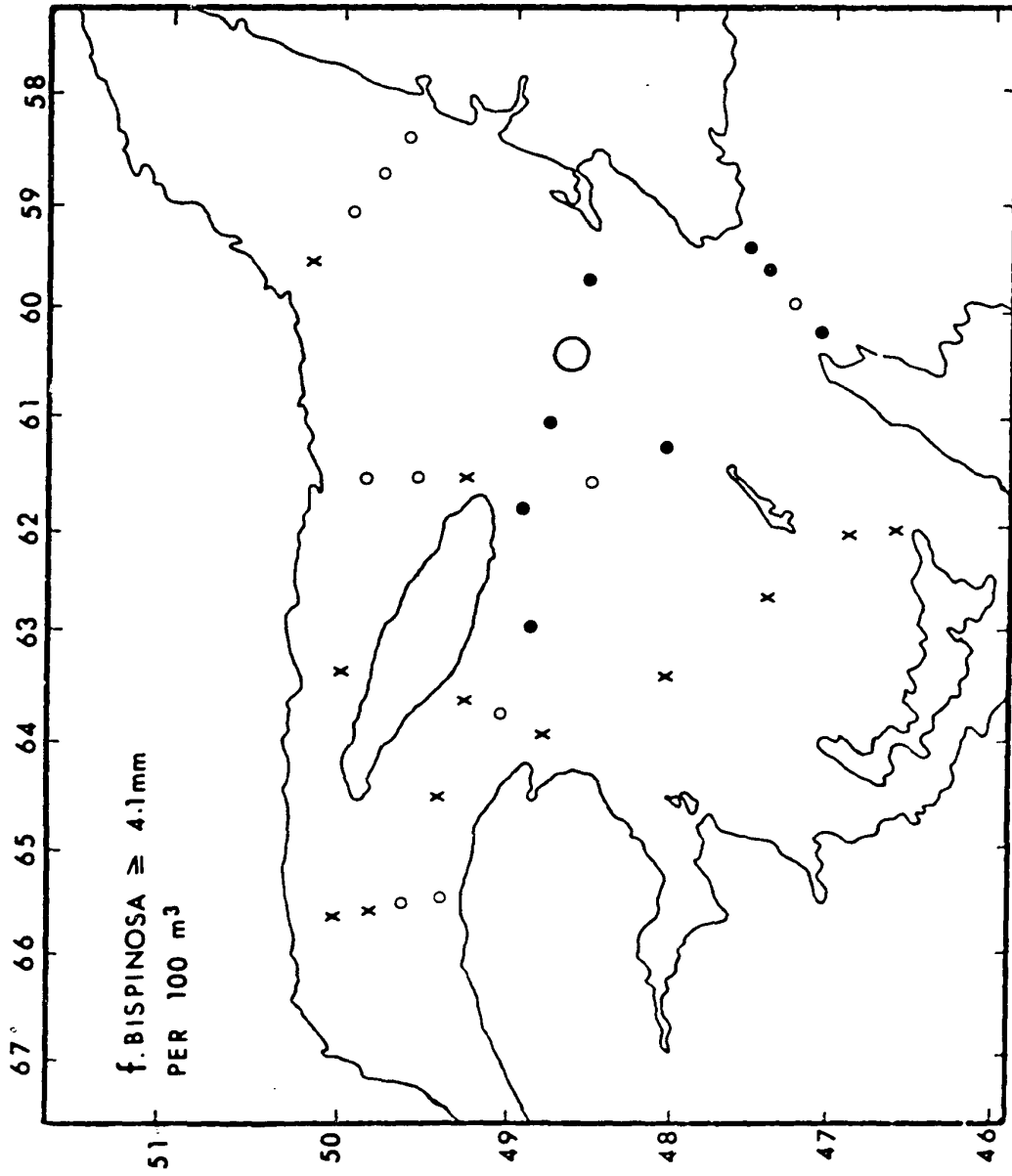


Figure 7. Parthemisto gaudichaudi (both forms). The averaged distribution per 100 cu m of individuals less than or equal to 4.0 mm. See Figure 3 for the code.

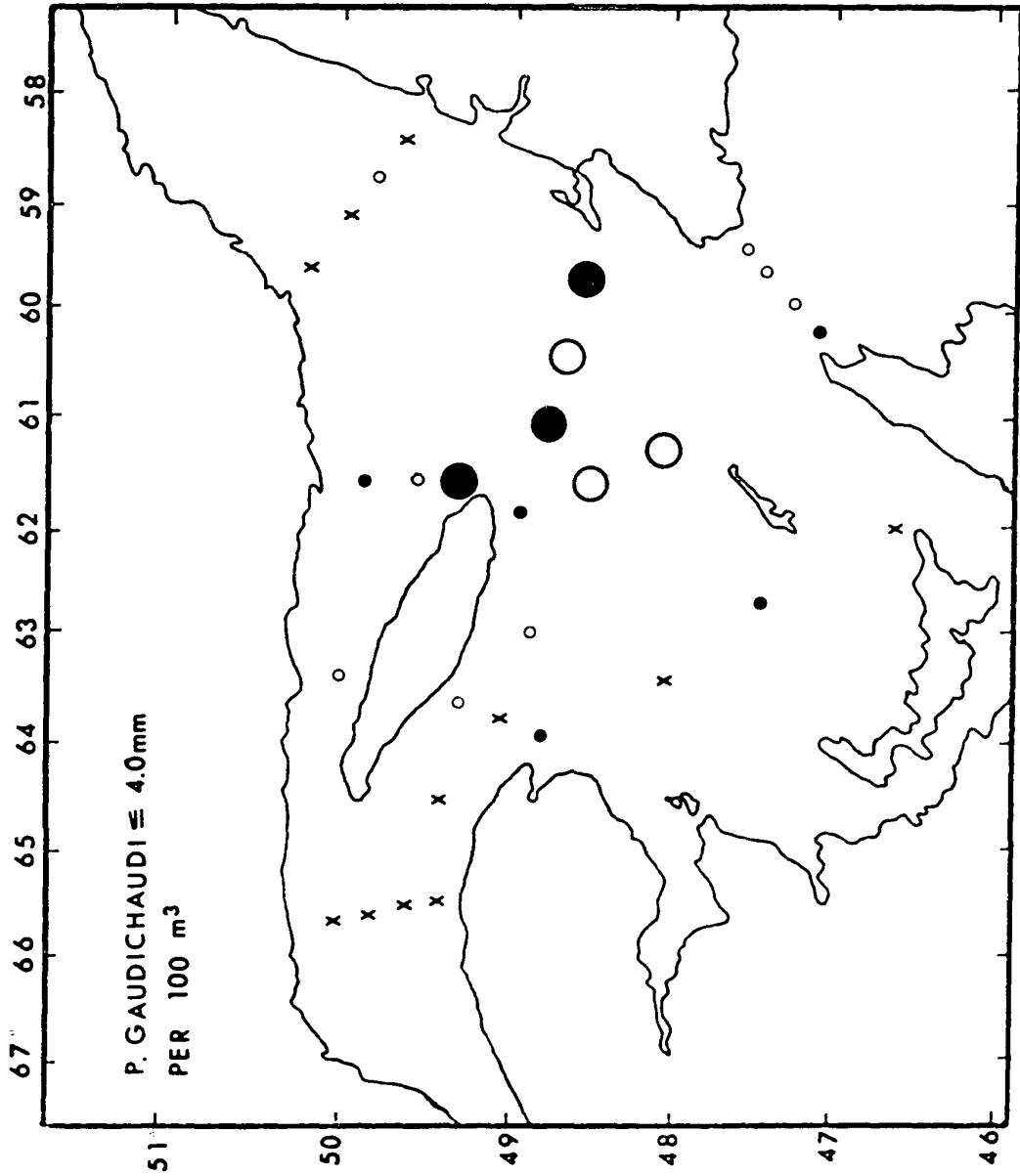


Table 2. The distribution in the Gulf of St. Lawrence of P. gaudichaudi less than or equal to 4.0 mm and of forms compressa and bispinosa greater than or equal to 4.1 mm.

Station	<u>P. gaudichaudi</u> less than or equal to 4.0 mm	form <u>bispinosa</u> greater than or equal to 4.1 mm	form <u>compressa</u> greater than or equal to 4.1 mm
1	5.515	6.816	7.814
2	1.415	1.618	4.994
3	1.494	4.793	5.081
4	1.535	3.879	14.186
5	0	.437	3.767
6	.369	.627	4.275
7	0	.381	4.802
8	0	0	3.964
9	10.042	.851	3.386
10	.604	.115	4.959
11	87.835	0	13.839
12	.104	0	.490
13	0	0	.234
14	0	0	.331
15	0	.124	.080
16	0	.058	.058
17	0	0	.108
18	.215	0	1.785
19	0	.156	.570
20	3.486	0	.482
21	0	0	0
22	3.535	0	3.716
23	0	0	1.150
24	13.274	0	1.031
25	.127	.194	1.634
26	7.309	1.255	14.484
27	13.918	.651	11.157
28	13.015	5.505	6.606
29	53.508	2.423	18.554
30	16.850	19.243	15.902
31	57.321	7.718	18.720

and the Strait of Belle Isle. At the same time, the currents are directed away from the Magdalen Shallows where both species are rare. The Shallows are fed instead by currents from the estuary (El-Sabh, Forrester and Johannessen, 1969).

The results indicate that bispinosa is insignificant in the Gulf. Bousfield (1951) also encountered this form only rarely in the Strait of Belle Isle although it was widely distributed in the offshore waters of Newfoundland. Pinhey (1927) also reported that the proportion of bispinosa to compressa in the offshore waters of Newfoundland was 3 to 1. Applying Bigelow's observation in 1926 that bispinosa is more oceanic than compressa, Bousfield (1951) related the minor importance of the former in the Strait to its sporadic presence in the coastal waters off Labrador, the result of which is that very few are swept into the Strait via the Labrador Current. Compressa, on the other hand, is found more regularly in the coastal regions and is consequently carried into the Strait in greater numbers.

Both forms enter Cabot Strait. As a result of its dual source compressa is evenly distributed over most of the eastern Gulf, as is P. abyssorum, whereas bispinosa is concentrated more in the southeast sections near Cabot Strait with very few at the northern stations 9, 10 and 11.

The ratio of abyssorum, compressa and bispinosa is approximately 6:3:1. Is the relative significance of the three then due to a varying tolerance of conditions inside the Gulf, or only a reflection of the

proportion in which they are carried into the Gulf? As Redfield and Beale (1940) have pointed out, the answer to this question can be determined by a comparison of the ratio inside the area studied and in the entry sites. If a varying tolerance is involved, then it will be reflected by a change in the ratio, whereas, if the animals are introduced in this same proportion, it will be reflected by a ratio that remains fairly constant as the amphipods invade deeper into the Gulf. The inflow through the straits is covered largely by stations 3, 4, 7 and 8. The ratios both from the areas of inflow as determined by the combined averages, and from the combined stations 9-12 and 25-31 inside the Gulf, were determined using only individuals greater than 4 mm.

The ratio of P. abyssorum to compressa is 1.54 to 1 in the straits and approximately 2 to 1 inside the Gulf. Therefore, the superiority of P. abyssorum in the Gulf of St. Lawrence is due only partially to its introduction in greater numbers. The proportion of this species also increases further inside the Gulf and either greater tolerance to Gulf conditions or greater breeding success, or both may contribute to this. The ratio of compressa to bispinosa remains fairly constant from the straits into the Gulf, indicating that few bispinosa are carried into the Gulf, for reasons already presented. The ratio is 3.097 to 1 in the straits in favour of compressa and 2.891 to 1 inside the Gulf, again in favour of the same form.

PART C. LIFE CYCLES AND GROWTH RATES

As a rule, organisms from high latitudes generally exhibit slower growth and consequently, greater longevity than their counterparts at lower latitudes, a pattern frequently resulting in a two-phase or even a polyphase breeding cycle. For example, Dunbar (1946) has reported a two-phase cycle for Parathemisto libellula in Baffin Island coastal waters with three generations co-existing during the reproductive season. Whatever the causes for such patterns in polar regions, they probably counteract the effects of slow growth and ensure a large population (Dunbar, 1941).

At lower latitudes, however, animals tend to grow faster and have a shorter life cycle. The two-phase and polyphase breeding patterns do not generally occur in warmer temperate waters (Dunbar, 1941) and simpler, one-phase, non-overlapping patterns are expected to predominate. This is, for example, the case with Sagitta elegans on the Atlantic coast of North America (Redfield and Beale, 1940). The species is believed to produce one brood per year in the Gulf of Maine and in the Gulf of St. Lawrence (Huntsman and Reid, 1921) but the same animal has a two-year cycle in the Canadian Eastern Arctic (Dunbar, 1941).

Bogorov (1940) has investigated the breeding pattern of Parathemisto abyssorum in the Barents Sea, and the usual high latitude cycle was reported. The present study provides its life history in the Gulf of St. Lawrence. Parathemisto gaudichaudi appears more sporadically in the Gulf, but as much as possible of its life cycle is examined.

It is assumed for this investigation that the Gulf of St. Lawrence

has a faunistic entity largely of its own and that the inflow of water is not sufficient to carry in organisms from a different population in numbers large enough to distort the size-frequency curves. In fact, the flow through Belle Isle Strait has been reported to be small indeed (Huntsman, Bailey and Hachey, 1954) and the net flow through Cabot Strait is outwards (McGregor, 1956). Figures 3-7 also show that a majority of the animals are inside the Gulf itself and not in the areas of inflow.

a. Parathemisto abyssorum

Life cycle.

Size-frequency curves were prepared for each cruise and the results are shown in Figure 8. The raw data, corrected to represent complete samples, are given in Table 3 of the text. It is clear from the bimodal distributions in Figures 8a, 8b and 8c that two distinct age groups are present in the Gulf during the spring and early summer. The individuals under the left curve represent juveniles and those under the right curve, the parent generation presumably yet to spawn. This bimodality disappears in late summer as the juveniles become older and the mature adults disappear from the plankton.

Judging from the increase in modal length from the first to the second cruise, the young grow from about 1.1-2.0 to 4.1-5.0 mm in approximately two or three weeks. Therefore, the total absence during the first cruise of any individuals 4.1-5.0 mm (or, for that

Figure 8. The size-frequency distribution of
P. abyssorum.

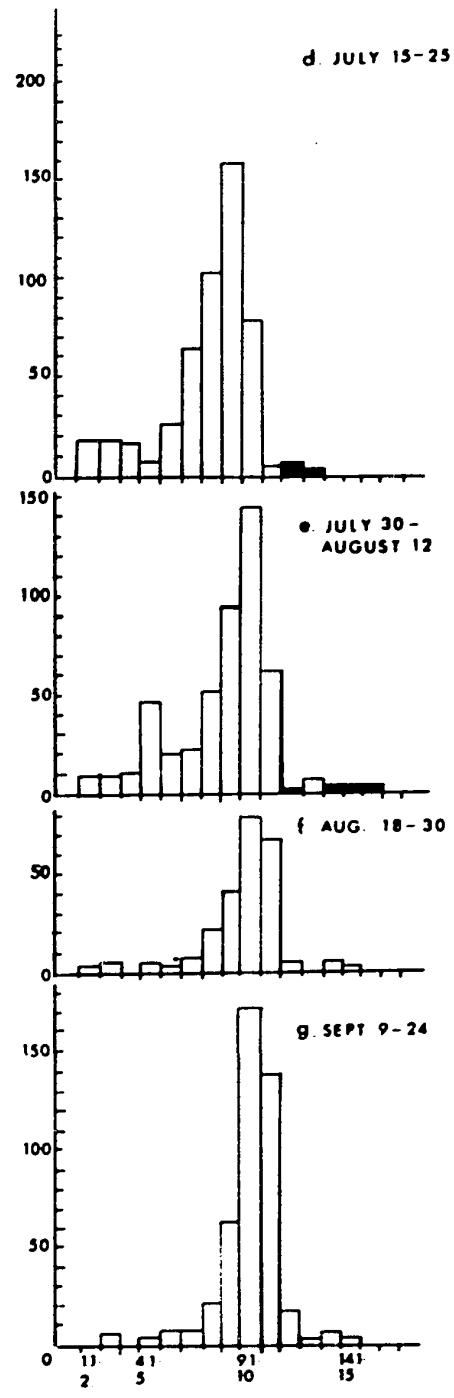
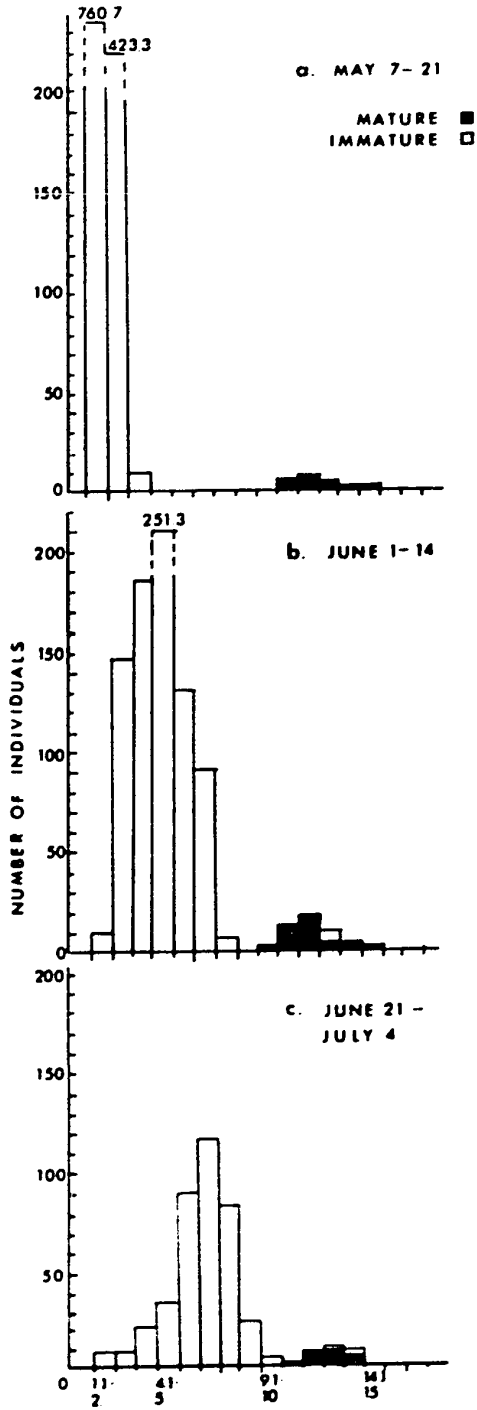


Table 3. The size-frequency distribution of Parathemisto abyssorum for each of the seven cruises. The collections had been previously subsampled and the numbers of individuals have been corrected to represent complete samples.

Sizes (mm)	Cruise						
	1	2	3	4	5	6	7
1.1-2.0	760.67	9.33	8	17.33	9.33	2.67	0
2.1-3.0	423.33	147.33	8	17.33	18.67	4	4
3.1-4.0	9.33	186.67	22.67	16	10.67	0	0
4.1-5.0	0	251.33	34.67	6.67	46.67	4	1.33
5.1-6.0	0	132	89.33	25.33	20	2.67	4
6.1-7.0	0	92	117.33	64	22.67	6.67	4
7.1-8.0	0	4	82.67	102.67	52	21.33	18.67
8.1-9.0	0	0	24	161.67	94.67	40	60
9.1-10.0	0	2.67	2.67	78.67	144	78.67	170.67
10.1-11.0	6.66	13.33	1.33	4	61.33	66.67	135.33
11.1-12.0	8	16.67	8	5.33	2.67	4	12
12.1-13.0	5.33	9.33	10.67	2.67	5.33	0	1.33
13.1-14.0	1.33	4	9.33	0	2.67	4	4
14.1-15.0	1.33	1.33	0	0	2.67	1.33	1.33
15.1-16.0	0	0	0	0	2.67	0	0

matter, of all individuals of intermediate lengths) makes it clear that the large spawning in early May is, in fact, the first spawning of the mature population. Figure 8 also shows that there is a continuous recruitment of young throughout the summer months, although on a very much smaller scale than during May. Furthermore, the small number of adults indicates that they die after spawning. At any rate, if this were not the case, and the adults did in fact survive to breed a second time, this would have resulted in a trimodal curve during the reproductive season. No mature adults remain by the time of the sixth cruise, and consequently no recently liberated young were collected during the seventh cruise. Bousfield (1951) however, did record juvenile and immature Parathemisto abyssorum in the Strait of Belle Isle as late as August and September.

Parathemisto abyssorum then is believed to adhere within the Gulf to a simple one-year life cycle in which the young are liberated from the brood pouch in spring by a generation destined to die after spawning. The juveniles grow rapidly during the spring and summer, but overwinter in an immature condition, not attaining sexual maturity until late winter or spring at which time they too will spawn and die. All but one of the large individuals under the right curve of Figure 8a, representing the first cruise, are mature, but the ratio of mature to immature individuals decreases over the summer until finally in late August and September, even the largest specimens are still immature. Table 4 illustrates this.

Table 4. The proportion of mature individuals of Parathemisto
abyssorum during each cruise.

Cruise	% <u>Parathemisto abyssorum</u> over 10.1 mm that are mature
1 (May 7-21)	94.10
2 (June 1-14)	88.10
3 (June 21-July 4)	81.80
4 (July 15-26)	50.00
5 (July 30-August 12)	18.98
6 (August 18-30)	0
7 (September 9-24)	0

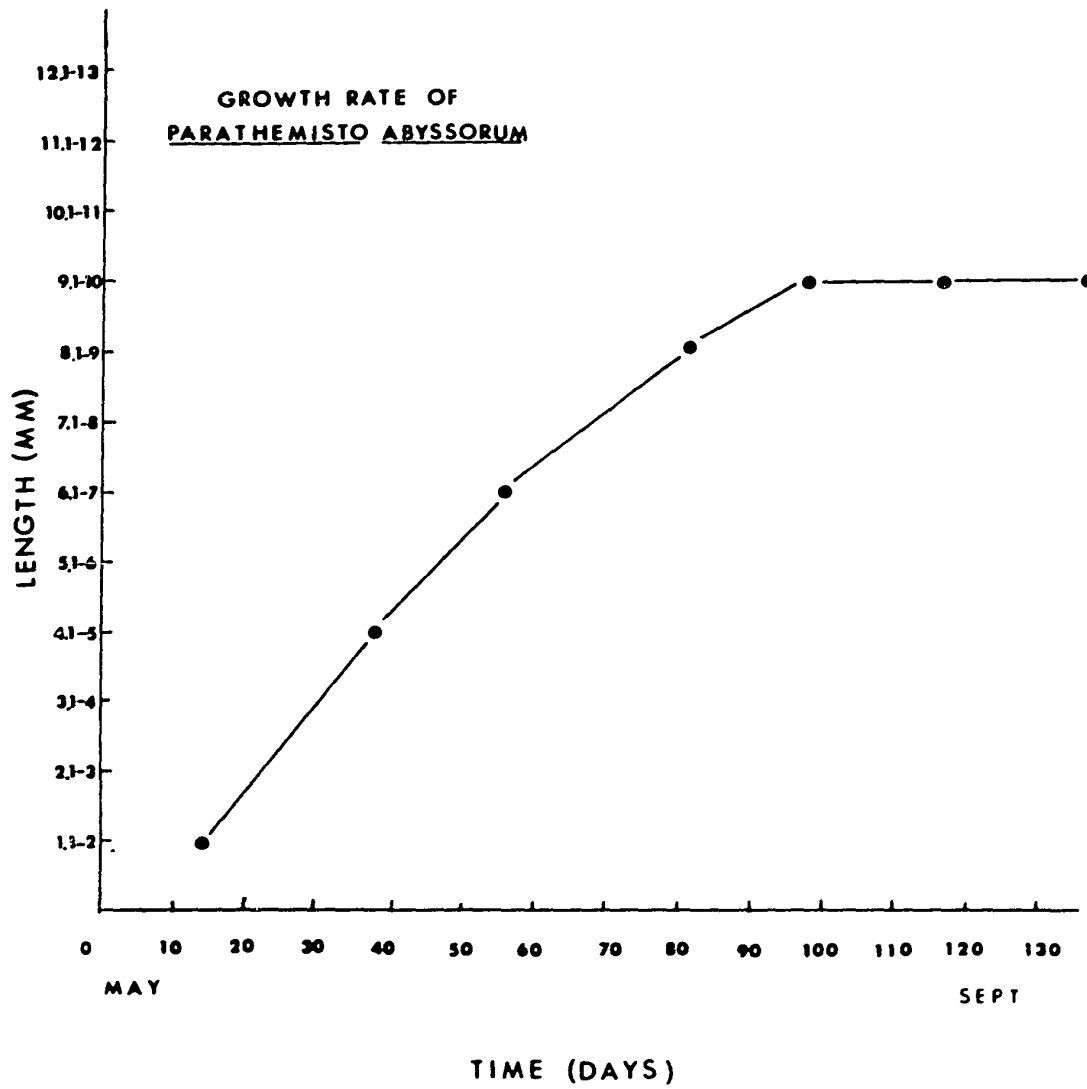
In contrast with this simple one-year pattern, Bogorov (1940), studying Parathemisto abyssorum in the Barents Sea, concluded that the animal has a life span of two years. He found large numbers of juveniles during the summer. From September to May, adults were present, presumably breeding in the spring. This much also describes its life cycle in the Gulf of St. Lawrence. Bogorov, however, found medium-sized individuals in his samples throughout the year, forming a third mode.

It must be mentioned that although spawning accounts for most of the spring reduction of the adult population in the Gulf, there is probably also a large loss over the winter. More problematic is the issue of net avoidance by larger individuals. It must be assumed in a study such as this that all segments of the population are equally sampled. Since great numbers of immature specimens as large as 10.1-11.0 mm were collected during the last few cruises, the assumption is probably a safe one.

Growth

The young are apparently liberated in May at a length of about 1.1-2.0 mm, and by early August, the modal length has increased to 9.1-10.0 mm. According to Figure 9, growth appears to be greatest in spring immediately after spawning and during the early summer. By late summer, the modal length of 9.1-10.0 mm is reached after which the growth curve flattens out. Although the modal length remains the same during the last three cruises, an increasing number of

Figure 9. The growth rate of P. abyssorum.

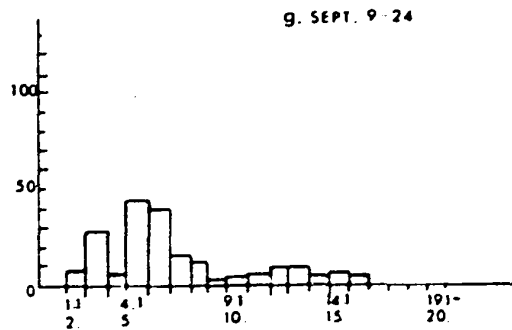
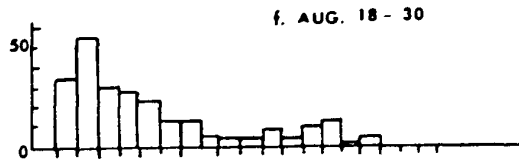
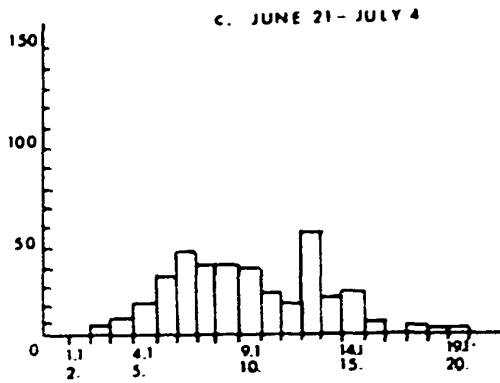
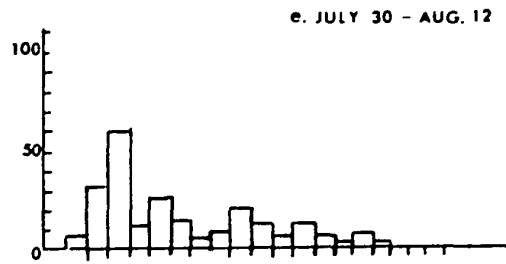
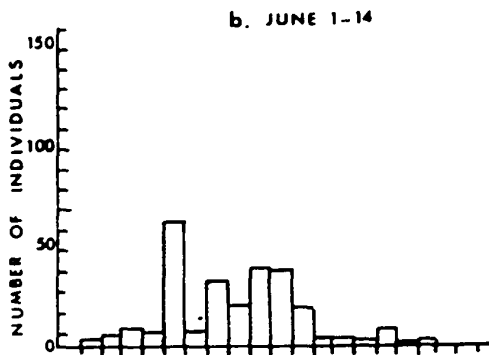
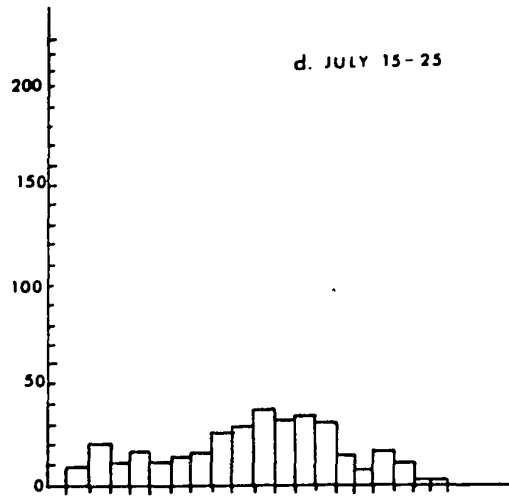
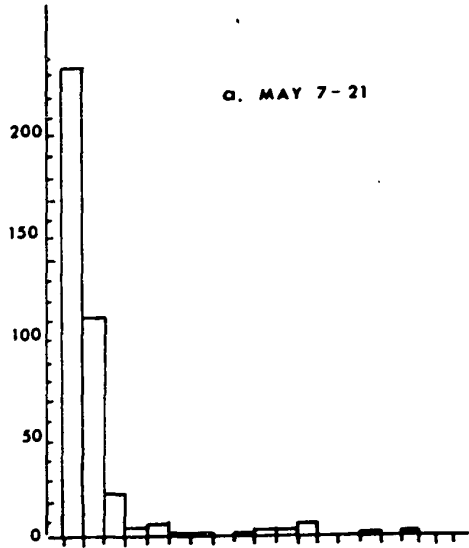


individuals attains that length. The parent generation of spring may be assumed to represent the immature population of the previous autumn, thereby indicating an increase in the modal length from 9.1-10.0 to 11.1-12.0 mm over the winter. The low growth rate during the autumn and winter is probably due to the energy expense required for the gradual maturation that takes place over this period. As has been reported for Parathemisto gaudichaudi by Kane (1963), the sexual maturity of Parathemisto abyssorum does not seem to correlate entirely with the size of the animal. Instead, it seems to be dictated by the progression of the seasons, and an individual of 10 mm that is collected in spring will probably be mature, whereas an individual of the same length collected in the fall will probably be immature.

b. Parathemisto gaudichaudi

Because neither form of Parathemisto gaudichaudi is abundant in the Gulf, it is difficult to construct and interpret size-frequency distributions for each of them. The low number of animals taken during each cruise results in curves which show little meaningful progression or consistency. Chi squares, applied to the distributions of the two forms were not significant. Therefore, the numbers of compressa and bispinosa were combined to produce the distributions that are shown in both Figures 10 and Table 5. Appendices IX and X give the separate distributions, omitting animals under 4 mm which were identified only as gaudichaudi.

Figure 10. The size-frequency distribution of
P. gaudichaudi. The degree of maturity is
not shown in these histograms.



LENGTH (MM)

Table 5. The size-frequency distribution of Parathemisto gaudichaudi from each of the seven cruises. The quantities of animals have been corrected to represent complete samples.

Sizes (mm)	Cruise						
	1	2	3	4	5	6	7
1.1-2.0	233.3	4	0	9.33	8	36	8
2.1-3.0	112	8	8	20	32	56	29.33
3.1-4.0	26.67	13.33	13.33	10.67	60	30.67	6.36
4.1-5.0	6	12	21.33	16	10.67	28	44
5.1-6.0	8	64	36	10.66	25.34	25.34	40
6.1-7.0	1.33	12	48	12	12	12	16
7.1-8.0	1.33	36	42.67	13.34	6.66	12	12
8.1-9.0	0	25.34	42.66	25.33	9.33	5.34	2.67
9.1-10.0	1.33	41.34	41.34	29.33	20	4	4
10.1-11.0	4	40.67	29.34	37.33	13.33	4	6.6
11.1-12.0	4	25.33	22.67	32	6.67	9.33	9.34
12.1-13.0	9.33	6.67	57.33	33.34	13.33	4	9.33
13.1-14.0	0	6.63	25.33	30.67	6.67	10.66	5.33
14.1-15.0	0	5.34	29.34	14.67	2.67	12	8
15.1-16.0	1.33	13.33	10.67	8	8	1.33	6.66
16.1-17.0	0	2.67	0	18.67	2.66	4	0
17.1-18.0	1.33	0	4	10.33	0	0	0
18.1-19.0	0	5.3	2.67	2.67	0	0	0
19.1-20.0	0	0	2.67	2.67	0	0	0
20.1-21.0	0	5.34	0	2.67	0	0	0
21.1-22.0	0	2.67	0	0	0	0	0

It is quite clear from the results that the young are released throughout the spring and summer and even into September, although by far the greatest amount are liberated during the first cruise in May. In slight contrast to this, Bigelow (1926) reported that within the Gulf of Maine, most of the breeding occurs in the summer. Bousfield (1951) found the same thing in the Strait of Belle Isle, but his samples covered only the months of July to September and he, therefore, cannot eliminate spring as the chief breeding season.

Studying the life history of the same species in the 0°-20°E sector of the Southern Atlantic Ocean, Kane (1966) reported a cycle similar to that which occurs in the Gulf of St. Lawrence. She found a large number of juveniles during the months of September and December and of immature specimens in March. The juveniles were 3-6 mm and consisted mainly of post-brood specimens, and so spawning appears to occur mainly in the spring months. There is also a protracted liberation of young during the early summer. During the winter, most of the animals were immature, but by late winter, 80.4% of the catch were mature, and presumably ready to spawn.

During the first cruise in the Gulf, 83.5% of the females over 10.1 mm were mature, but by the last cruise, 75% were immature. The decrease in mature females suggests that they die after spawning, although some mature animals do, in fact, survive and probably produce young later in the fall or in the subsequent spring. This contrasts with the life cycle of Parathemisto abyssorum in which virtually no mature animals are left in the Gulf by the time of the sixth and

seventh cruises.

Another explanation for the presence of large, immature individuals during the late summer and autumn is offered by Kane (1963), who studied the development of Parathemisto gaudichaudi and observed that a number of mature animals with full brood pouches were developing a second series of oocytes. This suggests that after spawning they will become temporarily immature, but will eventually produce a second brood either in the fall or in the subsequent spring. The absence of bimodality in the size-frequency curves and the hint of a blurred trimodality (see Figure 10), especially during the first three cruises when it would be most expected, suggests that this may be the case with some of the animals of this species in the Gulf.

PART D. FEEDING

Little work has been done concerning the feeding habits of Parathemisto or, for that matter, of any of the pelagic amphipods. Parathemisto is generally believed to be either carnivorous or omnivorous and the work that has been done to date confirms this.

Dunbar (1946) examined the gut contents of P. libellula and identified remnants of copepods, ostracods and other crustacea, including members of its own genus. Williamson (1950) observed P. gracilipes feeding on a fish larva, and Kane's work in 1962 with this same species also indicates that it is highly carnivorous and may be cannibalistic as well. Even the newly hatched appear to be

voracious carnivores; Conover (1960) observed the young of compressa swarming over a piece of dead euphausid.

a. Results.

At Logy Bay, Newfoundland, I observed the feeding habits of young P. abyssorum, all of which were under 5 mm. As workers have reported for other species of this genus, P. abyssorum is carnivorous, even in its early stages. Although the animals did not feed initially, they eventually accepted Artemia larvae, copepods, and occasionally fish larvae. They could be quite voracious at times. During the early stages of the experiments when forceps feeding was necessary, one individual ingested 48 Artemia larvae in just over an hour.

The actual feeding behaviour of P. abyssorum proved to be similar to that reported by Kane (1962) for P. gracilipes. The pleopods were never observed to handle the prey. Generally the prey organism is initially taken up by peraeopods 5-7, and then passed forward to the gnathopods which hold it against the mouthparts for mastication. Occasionally, as Bigelow (1926) also reported for different species of Parathemisto, the prey is swallowed whole.

The gut contents of compressa and bispinosa were analyzed specifically in order to determine whether the two forms differ in their food habits. Such a difference would be expected because of the exaggerated length of P5 of bispinosa -- a leg involved in

Table 6. Gut contents of compressa

No.	Gut contents
1	Crustacea remnants (copepods)
2	Crustacea remnants (copepods)
3	Crustacea remnants (copepods); unidentifiable organic material (UOM)
4	Crustacea remnants (copepods); UOM
5	Crustacea remnants (copepods, euphausids); UOM
6	Crustacea remnants (copepods)
7	Crustacea remnants (copepods); UOM
8	Crustacea remnants (copepods); UOM
9	Crustacea remnants (copepods); UOM
10	Crustacea remnants; UOM
11	UOM
12	UOM
13	Crustacea remnants (copepods); UOM
14	Crustacea remnants (copepods); UOM
15	Crustacea remnants; UOM
16	Crustacea remnants; UOM
17	Crustacea remnants (euphausids); UOM
18	Crustacea remnants (copepods); UOM
19	Crustacea remnants (euphausids); UOM
20	Crustacea remnants (euphausids); UOM

Table 7. Gut contents of bispinosa.

No.	Gut contents
1	Crustacea remnants (copepods)
2	Crustacea remnants (copepods)
3	Crustacea remnants (copepods)
4	Crustacea remnants (copepods); unidentifiable organic material (UOM)
5	Crustacea remnants (copepods); UOM
6	Crustacea remnants (copepods); UOM
7	Crustacea remnants (copepods); UOM
8	UOM
9	Crustacea remnants (copepods); UOM
10	Crustacea remnants (copepods); UOM
11	UOM
12	UOM
13	Crustacea remnants; UOM
14	Crustacea remnants (copepods)
15	Crustacea remnants; UOM
16	Crustacea remnants (copepods)
17	Crustacea remnants (copepods); UOM
18	Crustacea remnants (copepods)
19	Crustacea remnants; UOM
20	Crustacea remnants (copepods); UOM

prey capture. However, the results, shown in Tables 6 and 7, give no evidence of this. Unidentifiable organic material, believed to represent soft parts of prey, was found in most of the specimens. Of the 20 stomachs examined from each form, all but three of the bispinosa and all but two of the compressa had crustacea remains in their guts. Most of these were copepod appendages. Euphausiid remnants were found in the guts of four of the compressa. In general, however, the gut contents were very similar, although some of the soft material which remained unidentified might have provided some information to explain the function of the increased length of P5 of bispinosa.

PART E. SYSTEMATICS

The present genus Parathemisto was originally described as Themisto in 1825 by Guérin, a name subsequently changed to Euthemisto in 1887 by Bovallius because the name Themisto had been given to a nudibranch in 1815 (Kane, 1966). About the same time, Boeck (1870) described a separate genus Parathemisto. In 1924, Stephensen united Euthemisto and Parathemisto to create the genus Themisto, later corrected to Parathemisto by Barnard in 1930.

Within this genus, the species P. gaudichaudi has, above all others, provided systematists with problems since its initial identification by Guérin (1825). Early workers (Goës, 1865; Boeck, 1870; Sars, 1895; Stebbing, 1888; Vosseler, 1901; Bigelow, 1926) had divided P. gaudichaudi into two separate species,

namely P. compressa and P. bispinosa, but later authors (Stephensen, 1924; Mogk, 1927; Barnard, 1930, 1932; Dunbar, 1954; Hurley, 1955, 1960; Bowman, 1960) consider them one species, referring to them generally as subspecies or "morphs". Stephensen (1924) and later Mogk (1927), Barnard (1930, 1932) and Shen (1966) described an intermediate form between P. bispinosa and P. compressa which could not be clearly ascribed to either species. Stephensen concluded that previous authors who had considered these forms separate had been dealing, in fact, with extremes of the same species and he subsequently combined them to once again form the species P. gaudichaudi. It seems incorrect, however, to conclude that simply because "intermediate forms" exist, that the "extremes" do not represent different species, especially when the former are only a relatively small percentage of the latter. I shall attempt to show, therefore, that such "intermediate forms" exist even between species long accepted as valid.

a. Results

With only one exception of the length/width ratio of the fifth joint of P4 for individuals 4-7 mm, the degree of convergence is greater between compressa and P. abyssorum than between compressa and bispinosa for both the larger and smaller specimens. The greatest differences between compressa and bispinosa involve the fifth leg, the character emphasized by Stephensen (1924) when he combined the two. The frequency distributions for each character examined are shown in Figures 11-18 and the intergradation values are given in

Figure 11. The frequency distribution of the length ratio of joint 5, P5 to joint 5, P6 for females over 8 mm.

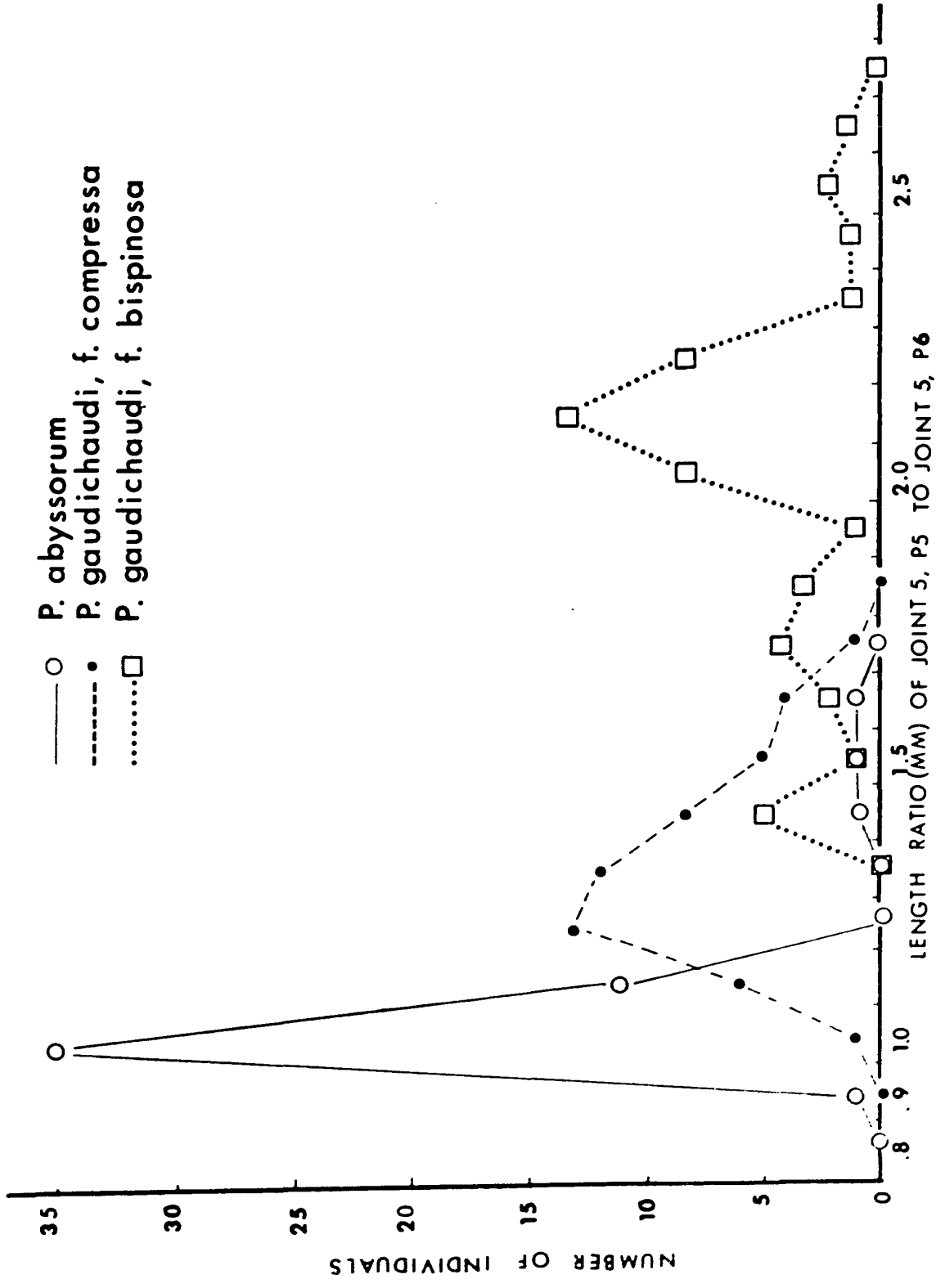


Figure 12. The frequency distribution of the length ratio of joint 6, P5 to joint 6, P6 for females over 8 mm. See Figure 11 for the code.

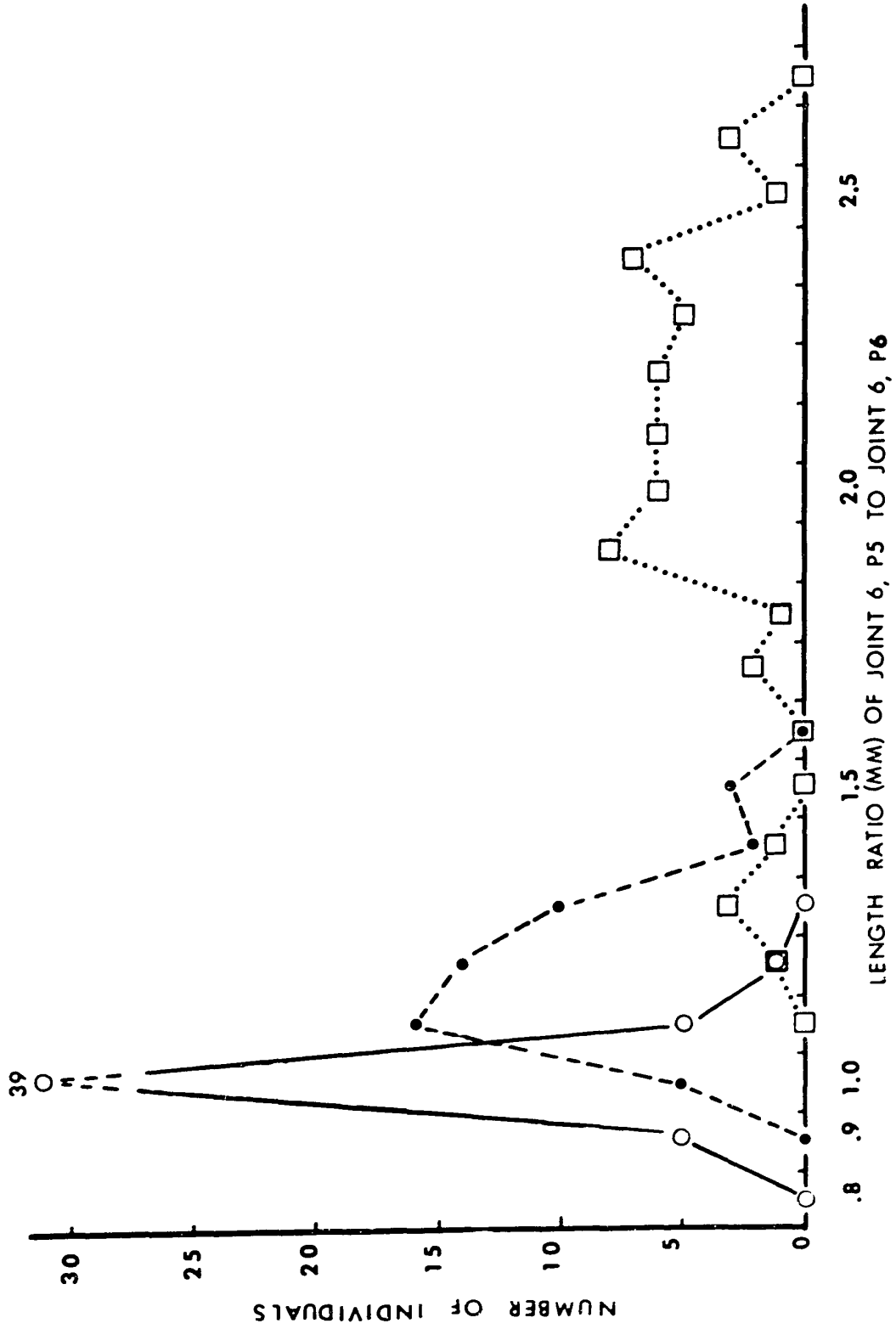


Figure 13. The frequency distribution of the length/width ratio of joint 5, P4 for females over 8 mm.
See Figure 11 for the code.

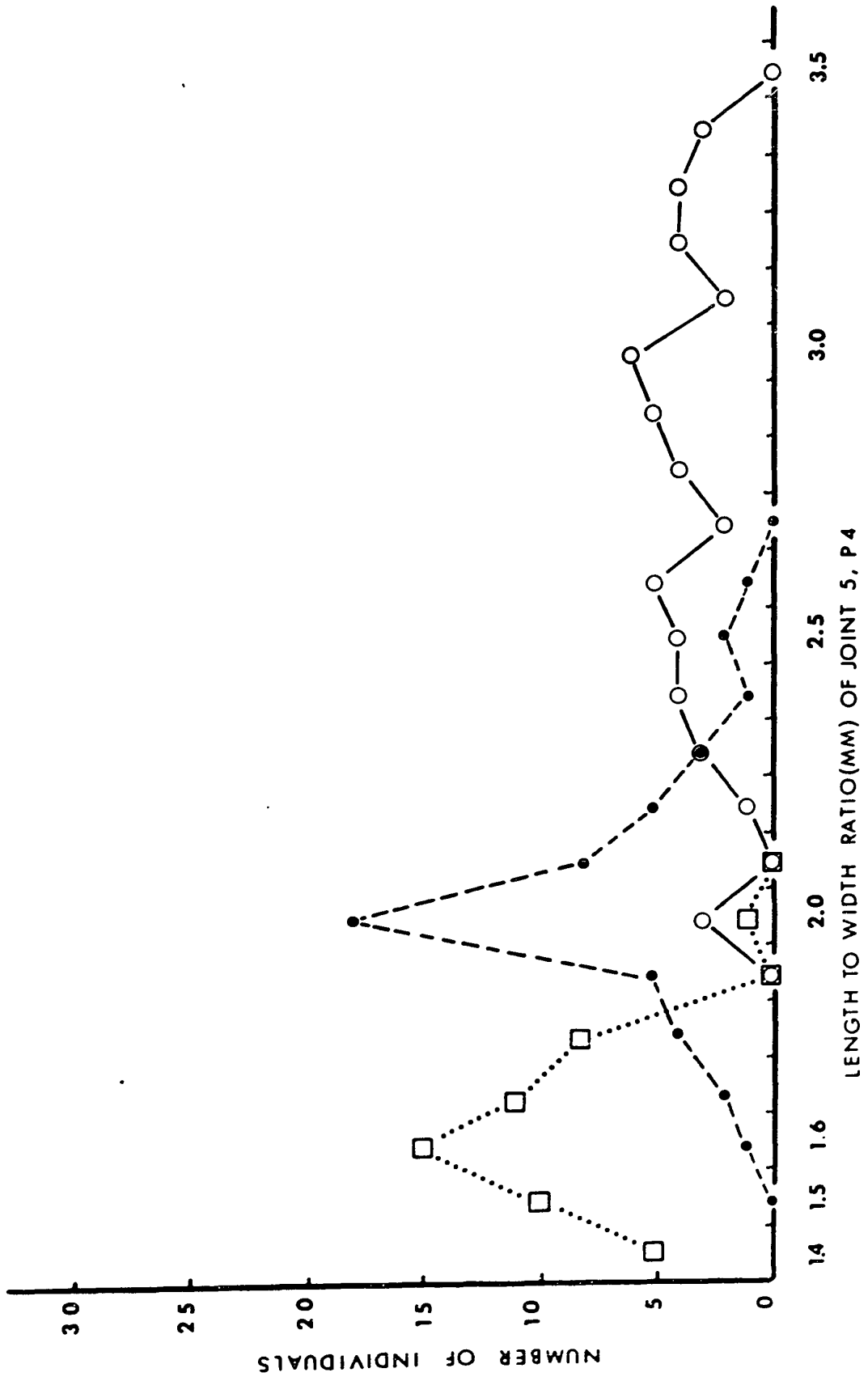


Figure 14. The frequency distribution of the length ratio
of joint 5, P5 to the body for females over
8 mm. See Figure 11 for the code.

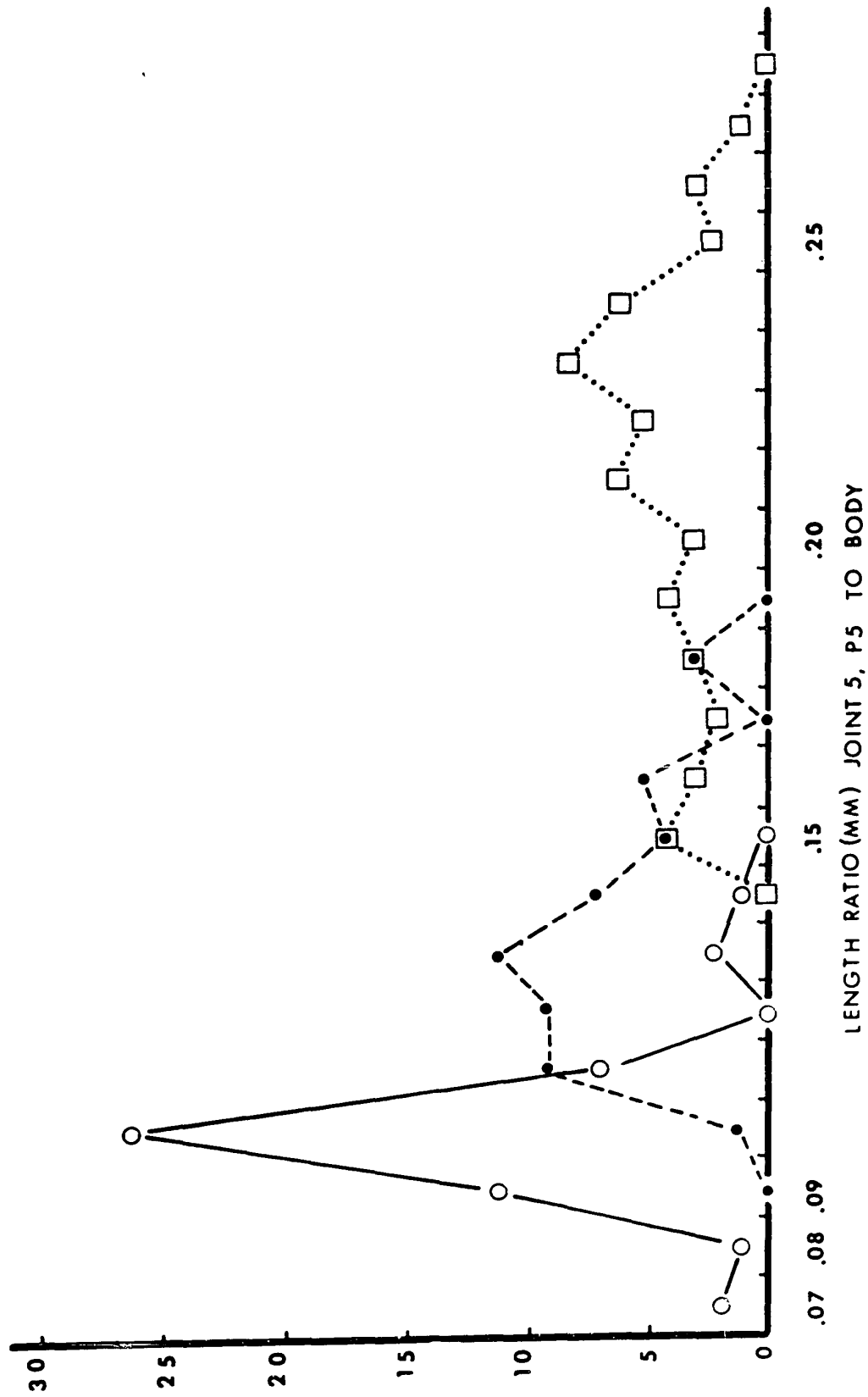


Figure 15. The frequency distribution of the length ratio of joint 5, P5 to joint 5, P6 for individuals 4-7 mm. See Figure 11 for the code.

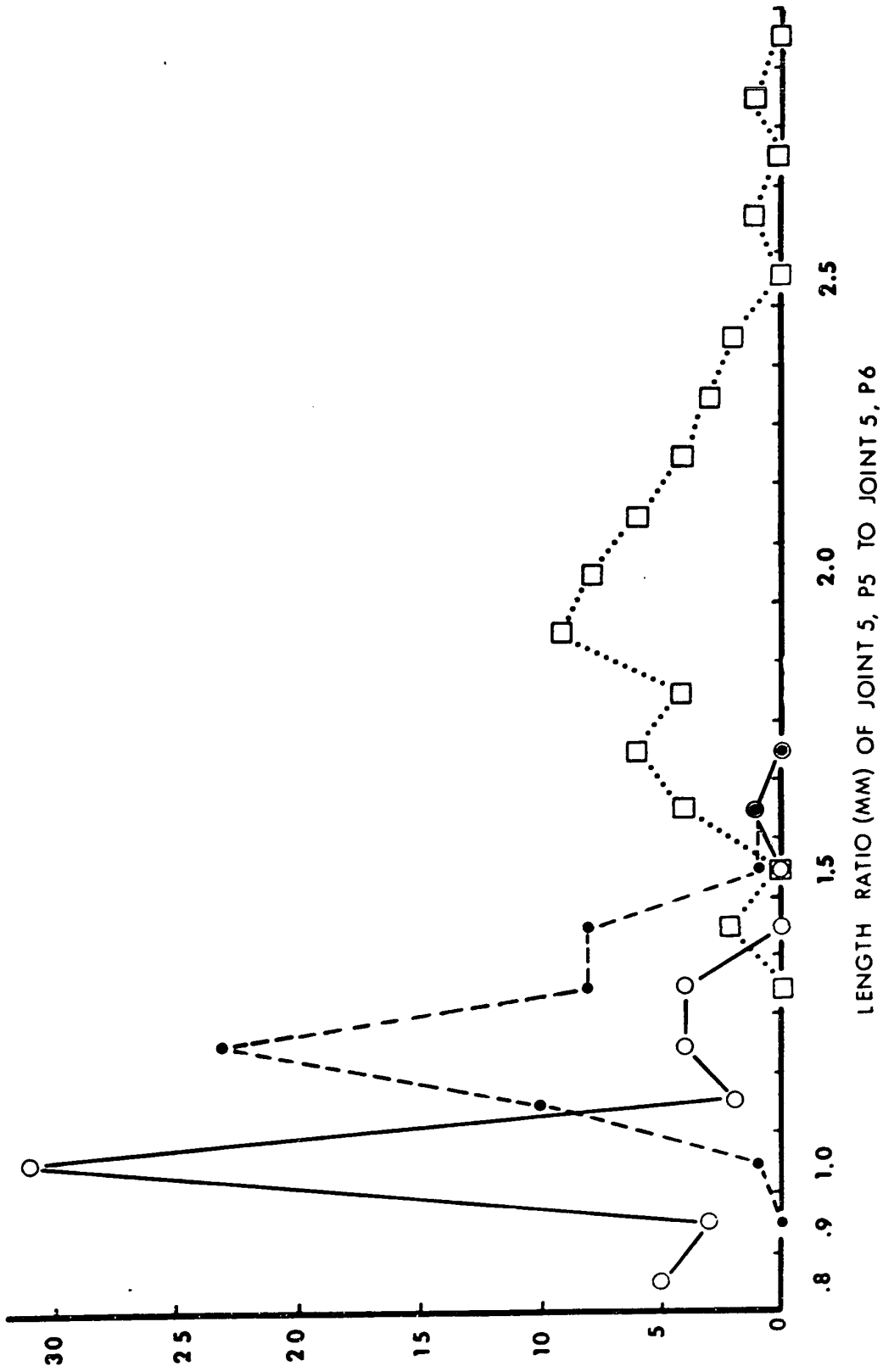


Figure 16. The frequency distribution of the length ratio of joint 6, P5 to joint 6, P6 for individuals 4-7 mm. See Figure 11 for the code.

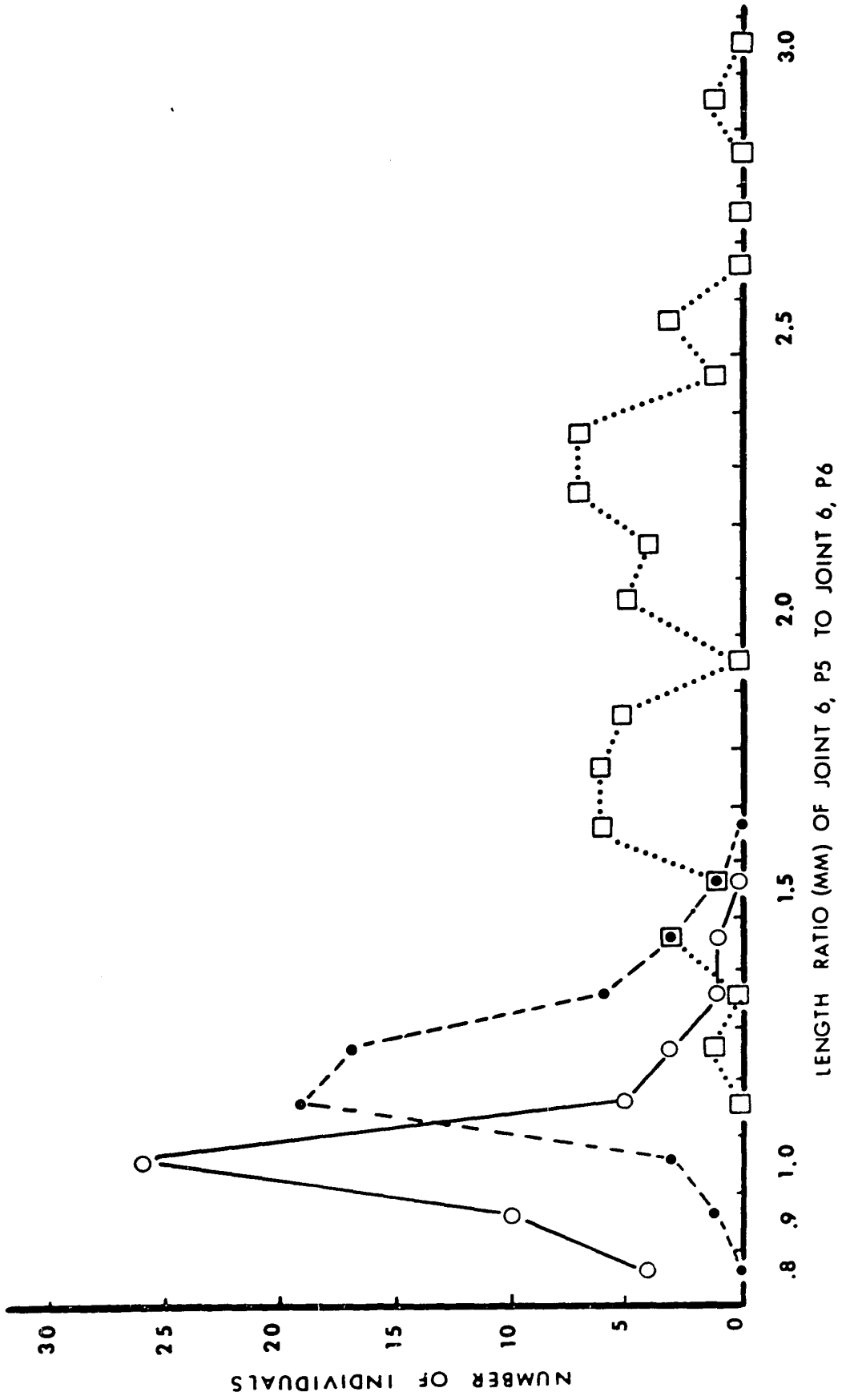


Figure 17. The frequency distribution of the length / width ratio of joint 5, P4 for individuals 4-7 mm.
See Figure 11 for the code.

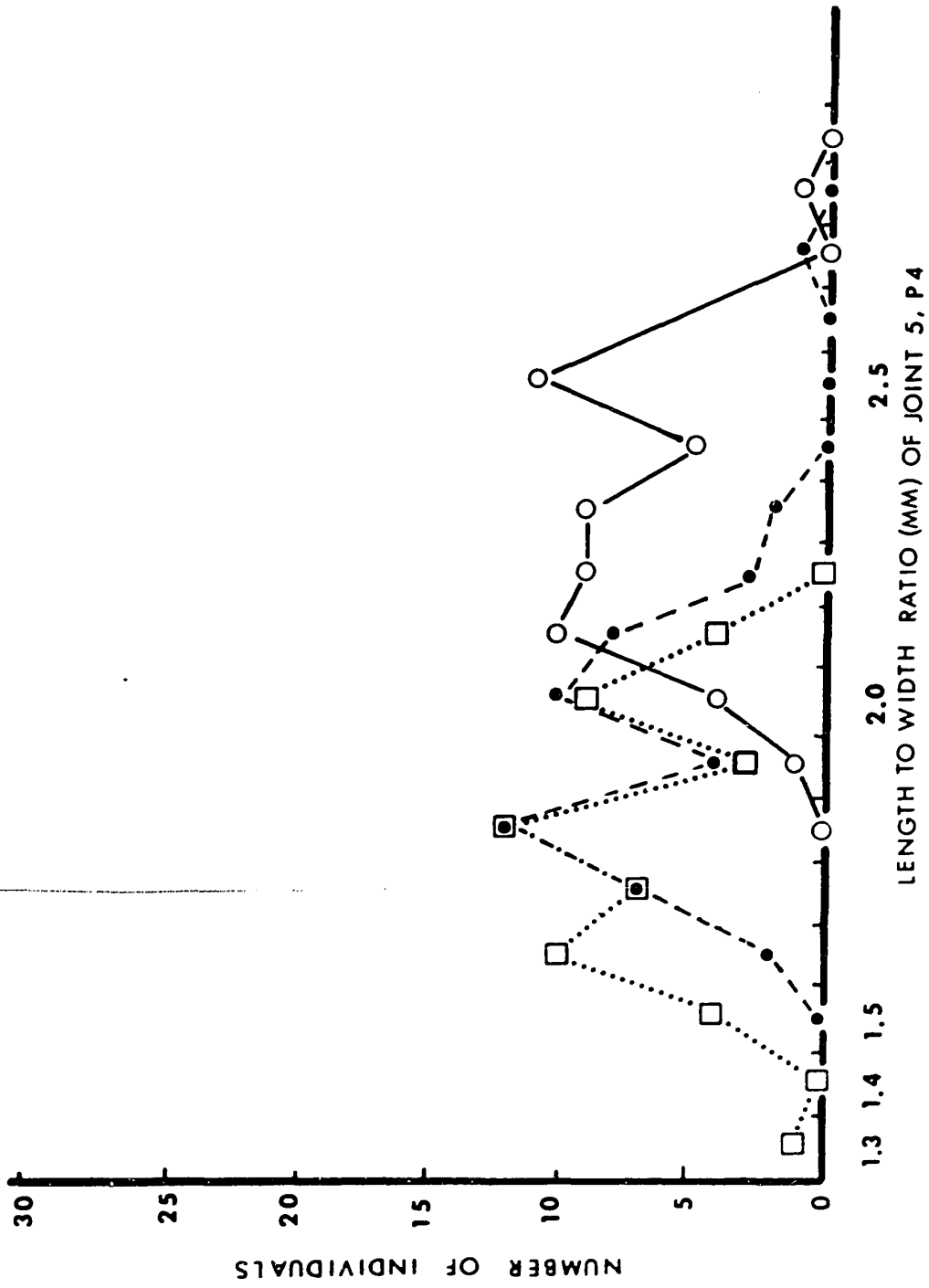


Figure 18. The frequency distribution of the length ratio
of joint 5, P5 to the body for individuals
4-7 mm. See Figure 11 for the code.

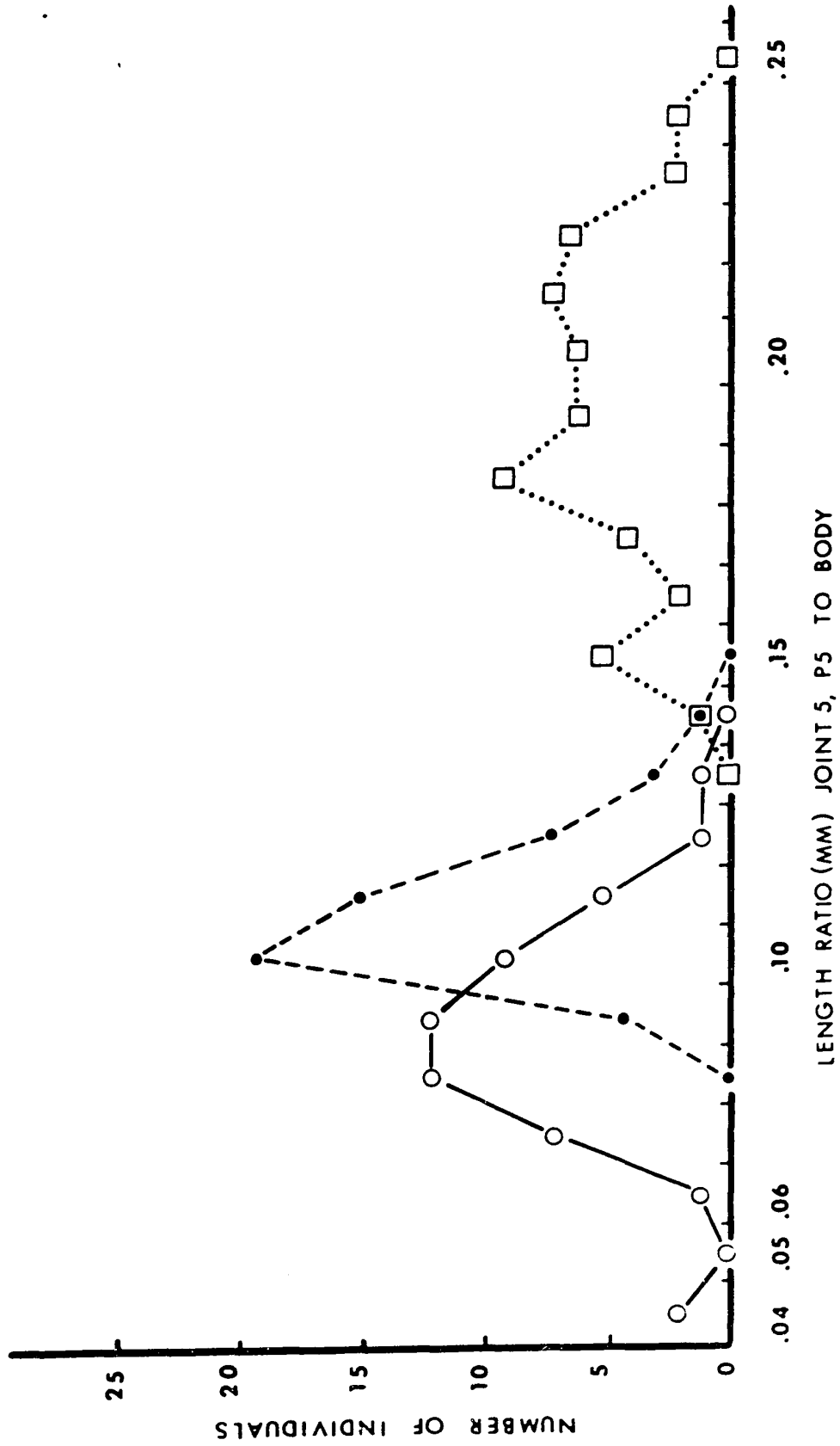


Table 8.

As Mayr (1964) points out, one of the major problems with morphological taxonomy is the difficulty in delimiting species from either subspecies or genera. Ginsberg (1938) offered 10% as the maximum convergence of a key character between two species. If this delimitation is accepted, then compressa and P. abyssorum would be considered as subspecies in two out of eight of the comparisons, whereas compressa and bispinosa would be considered as separate species in all but one of the comparisons. However, Ginsberg's definitions were arbitrary, and I would therefore hesitate to question the validity of the taxonomic separation of compressa and P. abyssorum as separate species. The larger divergence of compressa and bispinosa still requires an explanation however.

b. Discussion

An important factor to consider is the validity of using morphology as a basis for classification. Since it becomes highly impractical to define every species by an established reproductive isolation, workers must therefore resort to morphological grounds upon which to construct their classifications. Until recently, the judgements of affinity between groups of organisms were subjective and therefore quite variable from one worker to the next. Today, however, this subjectivity is beginning to be replaced by a relatively objective system of numerical taxonomy,

Table 8. Intergradation values

	form <u>compressa</u> vs <u>P. abyssorum</u>		form <u>compressa</u> vs form <u>bispinosa</u>	
	4 - 7 mm	females over 8 mm	4 - 7 mm	females over 8 mm
Jt 5, P5/Jt 5, P6	12%	10%	3%	8%
Jt 6, P5/Jt 6, P6	14%	11%	5%	5%
Jt 5, P5/body length	20%	11%	3%	10%
P4, length/width	18%	8%	over 18%*	8%

* The intergradation values could not be calculated from the frequency distributions in this case. A t-test was carried out instead between the means of these frequency distributions and those for the same character, between form compressa and P. abyssorum, 4-7 mm. From the results of the two, it could be determined that the intergradation values for the distribution in question was over 18% (see text).

some methods of which are discussed by Boyce (1964). It is because Stephensen (1924) combined P. bispinosa and P. compressa on purely morphological grounds that I have also resorted to morphology to re-establish the two as separate species, or at least to cast some doubts on their current classification.

The greater divergence of compressa and bispinosa would not be expected if they were indeed one species. Furthermore, the "intermediate form" between compressa and P. abyssorum has never inspired anyone to suggest that these two species are in fact one, and it therefore does not seem proper that P. bispinosa and P. compressa should have been combined on these same grounds.

It is generally believed that if two related species or two subspecies are sympatric, then, in order for them to successfully co-exist, they will have to be more dissimilar ecologically than if they were allopatric. Therefore, the results obtained would face possible discredit if compressa was sympatric only with bispinosa but allopatric in its relation to P. abyssorum, since then the greater divergence of bispinosa and compressa could be attributed to their sympatric existence and the similarities of the latter with P. abyssorum to their allopatry. The evidence drawn from the oblique samples, however, points to very similar horizontal distributions for all three. Furthermore, the few horizontal tows that were examined from the Strait of Belle Isle contained all three fairly often, indicating that their vertical distributions in the Gulf are not too dissimilar. In any case,

the actual individuals of compressa and P. abyssorum that were examined were from the same stations in the Strait of Belle Isle, whereas the specimens of bispinosa were from the central Gulf.

If bispinosa and compressa are generally sympatric, as they seem to be in the Gulf, it is difficult to understand how they can maintain their morphological integrity unless they are in fact two species and consequently do not interbreed. Alternatively, however, Nicholson (unpublished MS quoted by Kane, 1966) postulated a sex-linked factor that may genetically determine the two forms, indicating that the two are in fact part of a polymorphic system. His work has not been followed up, but if the ratio between the two forms proved to be constant from one station to the next, it would offer some support for this idea. The ratio in the Gulf varied, however, but this fails to disprove his hypothesis since differential tolerances of the two forms may alter the ratio in different areas of the Gulf.

Other workers (Bigelow and Sears, 1939; Bousfield, 1951) have observed that the eggs of form bispinosa and form compressa are indistinguishable with respect to shape, colour and size and that the individuals under 5 mm could not be ascribed to one or the other. However, the eggs of P. abyssorum have not yet been examined in detail and they seem to be not dissimilar to those of P. gaudichaudi. Furthermore, individuals of bispinosa measuring only 4 mm have been identified with ease. If progress is to be made in the proper classification of bispinosa and compressa

more work is highly desirable in the direction begun by Nicholson
and if possible this should include actual interbreeding experiments.

IV. SUMMARY

1. The genus Parathemisto in the Gulf of St. Lawrence is examined.
2. Its principal representatives in the Gulf are P. abyssorum and the two forms of P. gaudichaudi, compressa and bispinosa. Of these, P. abyssorum is dominant.
3. The concentration of these species in the central and eastern Gulf and their sporadic occurrence in the Magdalen Shallows result largely from the current system inside the Gulf.
4. P. abyssorum is believed to adhere to a simple one-year life cycle in which the parent generation dies after liberating its young in the spring.
5. The majority of P. gaudichaudi also release their young in the spring. It is not certain however whether the adults die after spawning; the presence of immature specimens as large as 21 mm supports the hypothesis of Kane (1963) that the parent generation may become secondarily and temporarily immature after spawning.
6. Compressa, bispinosa and P. abyssorum are carnivores, feeding mostly on copepods. Artemia and sometime fish larvae were also accepted by P. abyssorum in the laboratory. Euphausiid remains were occasionally identified in the gut of compressa.
7. From the gut content analysis, it appears that the feeding habits of compressa and bispinosa are very similar, leaving

the exaggerated length of the P5 of the latter unexplained.

8. Morphological evidence is presented to question the present classification of compressa and bispinosa as one species.

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APPENDIX I

"AMBROSE FOOTE" STATION POSITIONS

<u>Station</u>	<u>Longitude</u>	<u>Latitude</u>
1	60° 15' 00" W	47° 05' 55" N
2	59° 57' 35" W	47° 14' 35" N
3	59° 39' 00" W	47° 24' 30" N
4	59° 25' 30" W	47° 34' 43" N
5	58° 22' 20" W	49° 41' 30" N
6	58° 41' 45" W	49° 48' 50" N
7	59° 04' 40" W	50° 03' 40" N
8	59° 29' 00" W	50° 11' 30" N
9	61° 30' 30" W	49° 55' 15" N
10	61° 35' 00" W	49° 37' 00" N
11	61° 38' 30" W	49° 19' 30" N
12	63° 23' 30" W	49° 59' 36" N
13	65° 37' 14" W	50° 06' 40" N
14	65° 34' 00" W	49° 53' 55" N
15	65° 32' 30" W	49° 40' 05" N
16	65° 32' 25" W	49° 23' 30" N
17	64° 36' 20" W	49° 26' 50" N
18	63° 37' 40" W	49° 16' 12" N
19	63° 46' 20" W	49° 04' 45" N
20	64° 02' 00" W	48° 49' 40" N

Appendix I - continued

<u>Station</u>	<u>Longitude</u>	<u>Latitude</u>
21	63° 20' 55" W	48° 01' 45" N
22	62° 37' 00" W	47° 23' 05" N
23	62° 00' 00" W	46° 37' 00" N
24	61° 54' 50" W	46° 56' 00" N
25	62° 55' 33" W	48° 53' 05" N
26	61° 48' 05" W	48° 58' 00" N
27	61° 30' 20" W	48° 29' 00" N
28	61° 17' 00" W	48° 01' 20" N
29	60° 59' 40" W	48° 46' 25" N
30	60° 16' 40" W	48° 40' 15" N
31	59° 34' 00" W	48° 32' 40" N

APPENDIX II
CRUISES OF THE "AMBROSE FOOTE"

Cruise No.	1	2	3	4	5	6	7
Date	May 7- 21	June 1- 14	June 31- July 4	July 15- 26	July 30- Aug. 12	Aug. 18- 30	Sept. 9- 24
Stations examined	1	2	1	1	1	1	1
	2	3	2	2	2	2	2
	3	4	4	3	3	3	3
	5	5	5	4	4	4	4
	9	6	6	5	5	5	5
	10	7	7	6	6	6	6
	11	8	8	7	7	7	8
	12	9	9	8	9	8	9
	13	10	10	9	10	9	10
	14	12	11	10	11	10	12
	15	13	12	11	12	11	13
	18	14	13	12	13	12	14
	20	15	14	13	14	13	15
	21	16	15	15	15	14	16
	22	17	16	16	16	15	17
	23	18	17	17	17	16	18
		19	18	18	18	17	19
		20	19	19	19	18	20
		25	20	20	25	20	21
		26	25	21	26	25	22
		27	26	22	27	26	24
		28	29	23	28	29	
			30	24		30	
			31			31	

APPENDIX III

DEPTH OF SAMPLING

Cruise/ no.	Station no.	Sample	Depth (m)	Cruise/ no.	Station no.	Sample	Depth (m)
I/1		002	X*	II/15		170	250
I/2		003	X	II/16		176	312
I/3		005	240	II/17		181	296
I/5		010	75	II/18		188	220
I/9		023	90	II/19		193	X
I/10		030	250	II/20		199	120
I/11		032	60	II/25		206	275
I/12		035	125	II/26		213	63
I/13		040	140	II/27		216	319
I/14		045	125	II/28		222	49
I/15		051	214				
I/18		059	225	III/1		227	153
I/20		067	80	III/2		233	350
I/21		074	45	III/4		245	315
I/22		077	50	III/5		251	80
I/23		084	45	III/6		256	165
				III/7		262	250
II/2		095	300	III/8		269	90
II/3		104	450	III/9		277	51
II/4		107	312	III/10		284	188
II/5		120	81	III/11		292	54
II/6		125	184	III/12		299	100
II/7		130	250	III/13		307	162
II/8		137	143	III/14		313	200
II/9		142	55	III/15		320	208
II/10		148	110	III/16		325	323
II/12		155	115	III/17		334	331
II/13		158	150	III/18		353	187
II/14		164	113	III/19		347	355

Appendix III - continued

Cruise/Station no. no.	Sample	Depth (m)	Cruise/Station no. no.	Sample	Depth (m)
III/20	340	100	V/1	554	170
III/25	360	250	V/2	560	380
III/26	365	81	V/3	566	445
III/29	370	175	V/4	572	270
III/30	377	215	V/5	590	70
III/31	382	84	V/6	584	140
			V/7	578	175
IV/1	388	144	V/9	595	70
IV/2	395	382	V/10	600	240
IV/3	400	418	V/11	606	30
IV/4	410	269	V/12	612	125
IV/5	419	78	V/13	618	180
IV/6	434	188	V/14	624	185
IV/7	441	220	V/15	630	270
IV/8	447	85	V/16	636	240
IV/9	453	70	V/17	642	300
IV/10	458	270	V/18	648	250
IV/11	463	75	V/19	654	340
IV/12	469	113	V/20	660	135
IV/13	475	125	V/25	666	340
IV/15	490	250	V/26	672	110
IV/16	497	306	V/27	678	370
IV/17	502	344	V/28	684	70
IV/18	509	250			
IV/19	518	338	VI/1	690	150
IV/20	524	130	VI/2	696	370
IV/21	530	38	VI/3	702	375
IV/22	537	64	VI/4	708	300
IV/23	543	41	VI/5	720	75
IV/24	549	40	VI/6	726	150

Appendix III - continued

Cruise/Station no. no.	Sample	Depth (m)	Cruise/Station no. no.	Sample	Depth (m)
VI/7	738	228	VII/12	875	125
VI/8	732	86	VII/13	881	162
VI/9	744	80	VII/14	889	150
VI/10	750	262	VII/15	895	239
VI/11	756	53	VII/16	902	253
VI/12	762	113	VII/17	909	306
VI/13	770	144	VII/18	916	263
VI/14	775	132	VII/19	922	262
VI/15	779	298	VII/20	930	94
VI/16	785	297	VII/21	935	44
VI/17	789	300	VII/22	941	37
VI/18	795	231	VII/24	950	X
VI/20	807	112			
VI/25	813	313			
VI/26	818	81			
VI/29	824	135			
VI/30	830	219			
VI/31	836	69			
VII/1	955	153			
VII/2	961	413			
VII/3	969	388			
VII/4	975	325			
VII/5	852	44			
VII/6	842	153			
VII/8	849	100			
VII/9	864	44			
VII/10	869	268			

*Depths of these samples were not available.

APPENDIX IV

The distribution by station during each cruise of P. abyssorum greater than or equal to 4.1 mm. The figures here and in Appendices V to VIII represent numbers per 100 cu m and have been corrected to represent complete samples. "X" is shown if no sample was available.

Cruise	1	2	3	4	5	6	7
Station							
1	1.51	X	0	6.98	3.37	0	3.53
2	.51	7.90	9.73	6.54	5.23	5.37	4.82
3	0	11.15	X	3.07	13.53	0	.96
4	X	8.62	15.09	13.62	4.38	8.50	.64
5	0	1.90	0	17.23	6.05	3.06	0
6	X	4.81	7.14	X	16.86	11.08	17.86
7	X	7.30	9.23	53.49	21.74	16.01	X
8	X	.90	7.49	4.20	X	29.20	0
9	0	0	5.27	1.39	3.59	0	0
10	.81	5.54	24.38	25.17	18.4	0	50.15
11	0	X	3.09	10.64	42.78	2.44	X
12	0	1.02	.89	4.96	1.48	2.61	3.42
13	0	7.68	0	1.10	0	16.31	8.27
14	.57	6.65	0	X	12.10	1.48	13.74
15	2.79	2.45	.56	2.27	2.37	1.71	3.49
16	X	1.11	0	1.34	1.58	2.45	.71

Appendix IV - continued

Cruise	1	2	3	4	5	6	7
Station							
17	X	3.25	10.44	9.57	2.81	27.20	11.10
18	1.34	6.29	7.64	39.49	29.42	34.55	36.30
19	X	4.77	3.68	4.91	5.47	X	39.80
20	0	6.01	3.67	1.60	X	5.39	0
21	0	X	X	11.95	X	X	0
22	1.25	X	X	0	X	X	0
23	0	X	X	0	X	X	X
24	X	X	X	0	X	X	0
25	X	1.55	26.08	X	6.08	13.16	X
26	X	305.53	1.26	X	2.57	0	X
27	X	85.80	X	X	37.76	X	X
28	X	12.03	X	X	4.40	X	X
29	X	X	12.65	X	X	2.74	X
30	X	X	23.42	X	X	2.79	X
31	X	X	12.15	X	X	0	X

APPENDIX V

The distribution by station during each cruise of P. abyssorum
less than or equal to 4.0 mm.

Cruise	1	2	3	4	5	6	7
Station							
1	8.28	X	0	1.40	0	0	1.18
2	74.46	5.026	0	0	0	.67	0
3	51.62	512.992	X	0	0	0	0
4	X	2.352	1.08	0	0	0	0
5	0	2.85	1.03	2.15	1.01	0	0
6	X	2.75	0	X	1.02	0	0
7	X	7.30	0	0	0	2.78	X
8	X	1.80	0	0	X	0	0
9	0	.45	0	0	2.39	0	0
10	63.67	5.54	0	0	.92	1.24	0
11	628.47	X	0	30.14	9.36	4.88	X
12	5.10	22.35	.89	0	0	0	0
13	22.22	3.2	0	0	0	1.36	.83
14	1.72	12.74	0	X	0	0	0
15	3.72	.82	0	.45	0	0	0
16	X	1.11	0	.45	0	0	0
17	X	0	7.83	0	0	0	0
18	28.81	2.52	0	0	0	0	0
19	X	.48	.37	0	0	X	0

Appendix V - continued

Cruise	1	2	3	4	5	6	7
Station							
20	13.80	15.63	2.75	6.39	X	2.69	0
21	0	X	X	0	X	X	0
22	5	X	X	0	X	X	0
23	0	X	X	0	X	X	X
24	X	X	X	0	X	X	0
25	X	3.88	3.82	X	0	0	X
26	X	79.21	6.28	X	3.42	0	X
27	X	11.0	X	X	3.91	X	X
28	X	40.1	X	X	4.40	X	X
29	X	X	0	X	X	0	X
30	X	X	1.46	X	X	1.39	X
31	X	X	5.21	X	X	0	X

APPENDIX VI

The distribution by station during each cruise of form compressa greater than or equal to 4.1 mm.

Cruise	1	2	3	4	5	6	7
Station							
1	1.51	X	2.71	25.13	3.37	2.38	11.78
2	1.02	18.46	1.22	1.96	1.16	8.72	2.41
3	3.48	7.87	X	12.26	.90	1.17	4.80
4	X	36.06	36.65	3.59	5.6	0	3.19
5	0	0	0	11.85	3.03	6.12	5.38
6	X	0	1.59	X	5.11	9.24	5.45
7	X	10.94	0	6.84	4.83	1.39	X
8	X	3.59	6.13	2.80	X	7.30	0
9	0	0	5.27	1.39	0	2.14	14.90
10	0	.79	7.42	3.36	5.52	7.43	10.20
11	0	X	44.75	5.32	9.36	9.77	X
12	0	2.54	.89	0	0	0	0
13	0	.64	0	1.0	0	0	0
14	.57	.55	0	X	0	0	.86
15	0	0	.56	0	0	0	0
16	X	0	.35	0	0	0	0
17	X	.65	0	0	0	0	0
18	0	0	1.21	1.61	0	0	9.68
19	X	0	0	.49	1.56	X	.80

Appendix VI - continued

Cruise	1	2	3	4	5	6	7
Station							
20	1.97	0	.92	0	X	0	0
21	0	X	X	0	X	X	0
22	0	X	X	3.19	X	X	7.95
23	0	X	X	2.30	X	X	X
24	X	X	X	2.06	X	X	0
25	X	0	.64	X	2.03	3.87	X
26	X	45.26	7.54	X	5.14	0	X
27	X	13.2	X	X	9.11	X	X
28	X	0	X	X	13.21	X	X
29	X	X	31.62	X	X	5.49	X
30	X	X	9.52	X	X	22.29	X
31	X	X	3.47	X	X	33.97	X

APPENDIX VII

The distribution by station during each cruise of form bispinosa greater than or equal to 4.1 mm.

Cruise	1	2	3	4	5	6	7
Station							
1	1.51	X	0	27.92	6.74	1.19	3.53
2	0	1.42	4.86	1.31	.58	1.34	1.81
3	4.64	.66	X	19.42	0	1.17	2.88
4	X	5.49	12.94	3.59	.63	0	.64
5	0	0	0	0	0	3.06	0
6	X	0	0	X	.51	1.85	.78
7	X	0	0	0	1.21	.70	X
8	X	0	0	0	X	0	0
9	0	0	0	0	0	0	5.96
10	.81	0	0	0	0	0	0
11	0	X	0	0	0	0	X
12	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0
14	0	0	0	X	0	0	0
15	.31	0	.56	0	0	0	0
16	X	0	.35	0	0	0	0
17	X	0	0	0	0	0	0
18	0	0	0	0	0	0	0
19	X	0	0	0	.78	X	0
20	0	0	0	0	X	0	0

Appendix VII - continued

Cruise	1	2	3	4	5	6	7
Station							
21	0	X	X	0	X	X	0
22	0	X	X	0	X	X	0
23	0	X	X	0	X	X	X
24	X	X	X	0	X	X	0
25	X	0	0	X	0	.77	X
26	X	0	0	X	1.71	3.31	X
27	X	0	X	X	1.30	X	X
28	X	0	X	X	11.01	X	X
29	X	X	2.10	X	X	2.74	X
30	X	X	3.66	X	X	34.83	X
31	X	X	6.94	X	X	8.49	X

APPENDIX VIII

The distribution by station during each cruise of P. gaudichaudi
less than or equal to 4.0 mm.

Cruise	1	2	3	4	5	6	7
Station							
1	17.32	X	0	2.79	0	0	12.96
2	4.08	.42	0	3.60	0	0	1.81
3	1.74	1.31	X	.61	0	0	2.40
4	X	.78	4.31	.50	0	1.7	1.91
5	0	0	0	0	0	0	7.17
6	X	0	0	X	0	1.85	0
7	X	0	0	0	0	0	X
8	X	0	0	0	X	0	0
9	0	.45	0	0	0	4.29	65.56
10	0	0	0	1.68	0	0	2.55
11	415.43	X	0	8.87	2.67	12.21	X
12	.73	0	0	0	0	0	0
13	0	0	0	0	0	0	0
14	0	2.77	0	X	0	0	0
15	0	0	0	0	0	0	0
16	X	0	0	0	0	0	0
17	X	0	0	0	0	0	0
18	0	0	0	0	0	1.50	0
19	X	0	0	0	0	X	0
20	0	0	0	1.60	X	0	19.32

Appendix VIII - continued

Cruise	1	2	3	4	5	6	7
<hr/>							
Station							
21	0	X	X	0	X	X	0
22	0	X	X	0	X	X	10.60
23	0	X	X	0	X	X	X
24	0	X	X	22.67	X	X	3.88
25	X	0	0	X	.51	0	X
26	X	11.32	2.51	X	15.41	13.24	X
27	X	4.40	X	X	23.44	X	X
28	X	4.01	X	X	22.02	X	X
29	X	X	0	X	X	107.01	X
30	X	X	.73	X	X	32.04	X
31	X	X	0	X	X	114.64	X

APPENDIX IX

The size-frequency distribution during each cruise for form compressa greater than or equal to 4.1 mm. The numbers here and in Appendix X have been corrected to represent complete samples.

Cruise	1	2	3	4	5	6	7
Size (mm)							
4.1-5.0	16	12	21.33	16	5.33	12	40
5.1-6.0	2.67	62.67	22.67	9.33	10.67	10.67	30.67
6.1-7.0	1.33	10.67	42.67	10.67	6.67	8	16
7.1-8.0	1.33	36	32	6.67	5.33	9.33	8
8.1-9.0	0	22.67	29.33	17.33	5.33	2.67	2.67
9.1-10.0	1.33	30.67	34.67	21.33	16	1.33	2.67
10.1-11.0	2.67	38	26.67	20	12	1.33	5.33
11.1-12.0	1.33	25.33	20	20	6.67	8	6.67
12.1-13.0	5.33	6.67	49.33	26.67	13.33	4	9.33
13.1-14.0	0	6.67	20	10.67	6.67	9.33	5.33
14.1-15.0	0	2.67	26.67	8	2.67	10.67	8
15.1-16.0	0	13.33	10.67	5.33	6.67	1.33	5.33
16.1-17.0	0	2.67	0	10.67	1.33	4	0
17.1-18.0	0	0	4	2.33	0	0	0
18.1-19.0	0	5.3	2.67	0	0	0	0
19.1-20.0	0	0	0	0	0	0	0
20.1-21.0	0	2.67	0	0	0	0	0
21.1-22.0	0	2.67	0	0	0	0	0

APPENDIX X

The size-frequency distribution during each cruise of form bispinosa greater than or equal to 4.1 mm.

Cruise	1	2	3	4	5	6	7
Size (mm)							
4.1-5.0	0	0	0	0	5.33	16	4
5.1-6.0	5.33	1.33	13.33	1.33	14.67	14.67	9.33
6.1-7.0	0	1.33	5.33	1.33	5.33	4	0
7.1-8.0	0	0	10.67	6.67	1.33	2.67	4
8.1-9.0	0	2.67	13.33	8	4	2.67	0
9.1-10.0	0	10.67	6.67	8	4	2.67	1.33
10.1-11.0	1.33	2.67	2.67	17.33	1.33	2.67	1.33
11.1-12.0	2.67	0	2.67	12.0	0	1.33	2.67
12.1-13.0	4	0	8.0	6.67	0	0	0
13.1-14.0	0	0	5.33	20	0	1.33	0
14.1-15.0	0	2.67	2.67	6.67	0	1.33	0
15.1-16.0	1.33	0	0	2.67	1.33	0	1.33
16.1-17.0	0	0	0	8	1.33	0	0
17.1-18.0	1.33	0	0	8	0	0	0
18.1-19.0	0	0	0	2.67	0	0	0
19.1-20.0	0	0	2.67	2.67	0	0	0
20.1-21.0	0	2.67	0	2.67	0	0	0
21.1-22.0	0	0	0	0	0	0	0