Ecology and Distribution of Some Pelagic Hyperiidea (Crustacea, Amphipoda) from New Zealand Waters

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THE MARINE pelagic Amphipoda recorded from New Zealand have been discussed systematically (Stephensen, 1927; Barnard, 1930, 1932; Hurley, 1955), but few data are available on their distribution and ecology. The situation in Australia (Barnard, 1931; Dakin and Colefax, 1933, 1940) and South Africa (Stebbing, 1910; Barnard, 1916, 1925, 1940) is similar. However, in antarctic latitudes some features of the ecology of amphipods have been fairly extensively treated (Mackintosh, 1934, 1937; Hardy and Gunther, 1935).

The data presented herein are of collections made from the survey-frigate H.M.N.Z.S. "Lachlan," in southern New Zealand waters, during the summer of 1951. The hyperiids from these collections have been identified by D. E. Hurley, who generously undertook this taxonomic study (Hurley, 1955).

Fourteen species were present in the collections. Seven of these were new records for New Zealand. Five species, namely, *Parathemisto* (*Euthemisto*) *gaudichaudii* (Guer.), *P. australis* (Stebbing), *P. gracilipes* (Norman), *Cyllopus magellanicus* Dana, and *C. macropis* Bovallius, were present in sufficient numbers to permit discussing some features of their ecology, especially their relationships to the water masses in the area about southern New Zealand. The remaining nine species were of rare occurrence, although their biological and environmental associations provoke discussion.

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MATERIAL AND METHODS

Details of the areas from which collections were made, the gear and the methods, are discussed elsewhere (Bary, 1956, 1959). The areas sampled extended between Wellington and Dunedin (one cruise in January, a second in March, 1951), between Dunedin and Foveaux Strait (during January through March), and between Wellington and Auckland and Campbell islands, about 400 miles south of New Zealand (one cruise, November, 1951). (See Figs. 5, 6.) Procedure and gear were standardized: tows were of 3 minutes at 1½ to 2 knots, within the surface metre of water, using a net of graded silks, 50 cm. in diameter. Of the 80 samples, those of Stations 74–85 were collected whilst the ship was at anchor overnight in a tidal stream in western Foveaux Strait (Bary, 1956). Although the temperature was taken at each of these, salinity was determined only for Station 79. Therefore, only this station is shown in the various figures. All of the rare species collected at Stations 74–85 are shown as being captured at Station 79 in Figures 2, 5*a*. Of the common species, only those captured at Station 79 are illustrated. All samples have been quantitatively analysed.

The method of the temperature–salinity–plankton (T–S–P) diagram (Bary, 1959) is used here to elucidate the distributions of species. Occurrences of species are plotted in the intercepts of the temperatures and salinities of the stations at which they were captured. Species are thus related to the hydrological conditions as indicated by these properties. The water-envelope (Figs. 1–4) surrounds the intercepts of all the temperatures and salinities of the surface waters in the sampled areas, but Figure 1 shows only those for plankton stations. The hydrology of the area and the relationships of these waters are illustrated and discussed by Bary (1959).

T–S–P diagrams of the five commonly occurring amphipods are shown in Figures 3 and 4. The geographical distributions of these species in relation to temperatures (Figs. 5, 6) are discussed and interpreted in the light of information derived from the T–S–P diagrams. The stations have been subdivided into several series, and each of these is as near as possible a synoptic series and a geographic unit. The geographical distribution of the subantarctic species and the coastal–subtropical species are charted for each series. Rare species are charted according to the water properties with which they are associated in the T–S–P diagram (Fig. 2). Thus, *Vibilia stebbingi* (?), at Station 210, is shown to be in water of subantarctic origin in the T–S–P diagram; therefore, the appropriate geographical chart is that which concerns other subantarctic species (Fig. 5*g*). As well, the rare species are listed in Table 1 and appreciations are made of their distributions as recorded by other investigators, and as indicated by the relationships exhibited in the T–S–P diagrams. In the charts they are shown together at Station 79 among the subtropical species.

DISTRIBUTION

Indicator groups of species were selected previously (Bary, 1959) for coastal water (one group), for water originating in the subtropical region (one group), and for the subantarctic region (two groups, a Southern Group for cold water, and a Northern Group for that cold water which has undergone a temperature increase in its progress northward). The cohesion of each of these groups in the T–S–P diagrams can only be interpreted as being due to a correlation between the distribution of the individual species composing the group and the properties of the water body which they inhabit and of which they are indicators. The area of chief concentration of each indicator group of species is shown in Figure 2 by lining-in; there are, however, no species of the Northern Group among the Amphipoda. The stippled arrows indicate the routes (within the diagram) along which oceanic species are believed to be penetrating towards coastal waters. These routes closely coincide with the direction of water movements as deduced from the corresponding T–S diagram of the surface waters (Fig. 1).

The cold-water Amphipoda are represented solely by species of the Southern Subantarctic Group (Fig. 3). Large numbers of *Parathemisto* (*Euthemisto*) *gaudichaudii* were captured; there were fewer specimens of *Cyllopus magellanicus*, and *C. macropis* was rare. Both the numbers of these oceanic species, and the frequency of their occurrences decreased in coastal waters, probably as a result of their being transferred into relatively adverse conditions. However, the greater number of the stations in coastal waters were occupied in daylight (Fig. 1) which may contribute towards the taking of fewer specimens (this feature is discussed by Bary, 1959).

The occurrences of two Coastal species, *Parathemisto gracilipes* and *P. australis*, and of the subtropical species, *Hyperoche mediterranea* Senna, are shown in Figure 4. *Hyperoche mediterranea* is restricted to a narrow range of temperature in the warmest waters (except for Station 100) whilst *P. gracilipes* and *P. australis* occur commonly over much the same salinities, but over a wider range of temperatures.

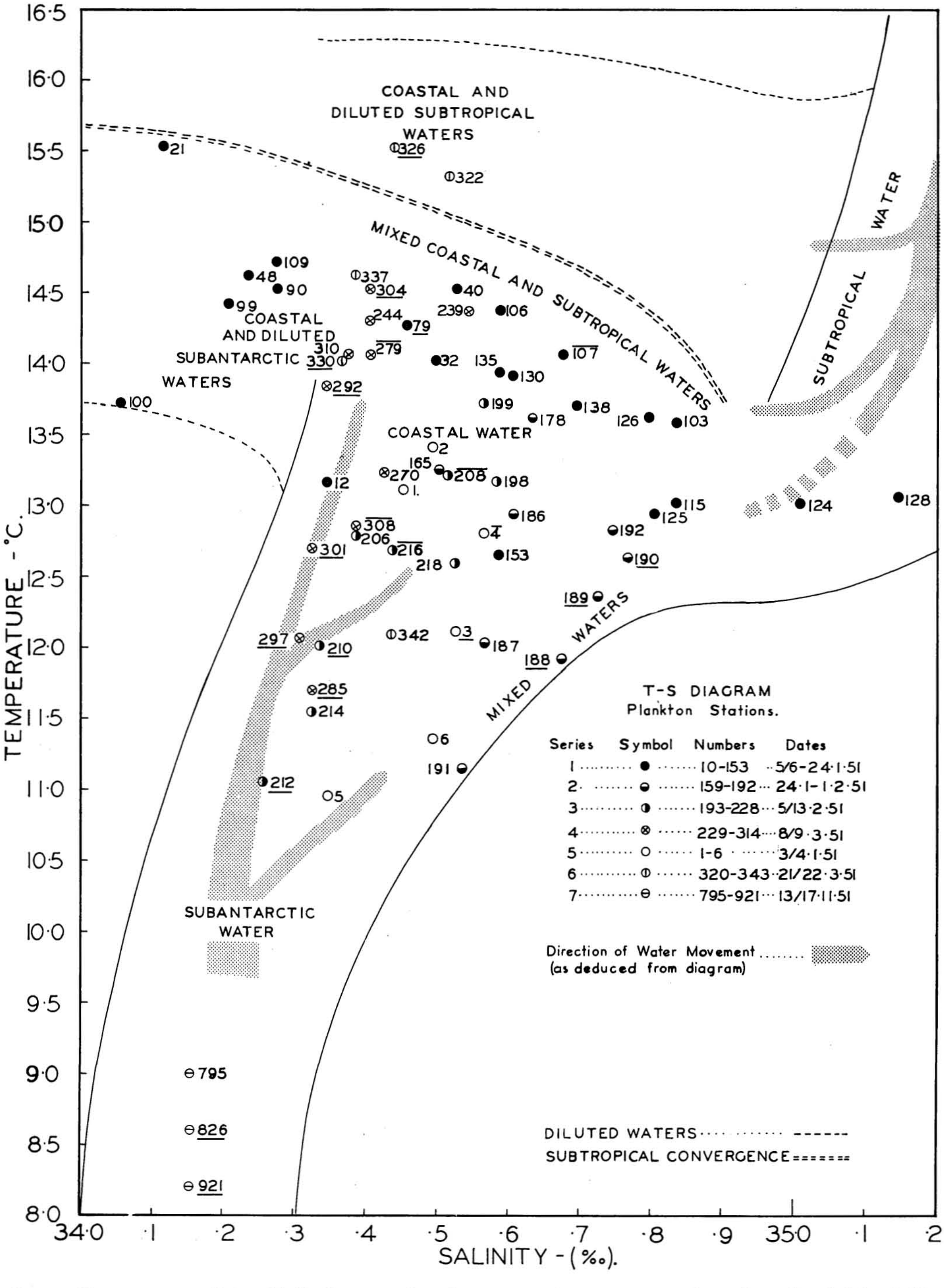


FIG. 1. Temperature–salinity (T–S) diagram of surface waters about eastern and southern South Island, New Zealand, extending southwards to Auckland and Campbell Islands. Plankton stations for which temperatures and salinities were obtained are entered. Numbers underlined (e.g., 212) represent night stations; numbers overlined represent stations between dawn and sunrise or sunset and dark. Stations without lines were occupied in daylight.

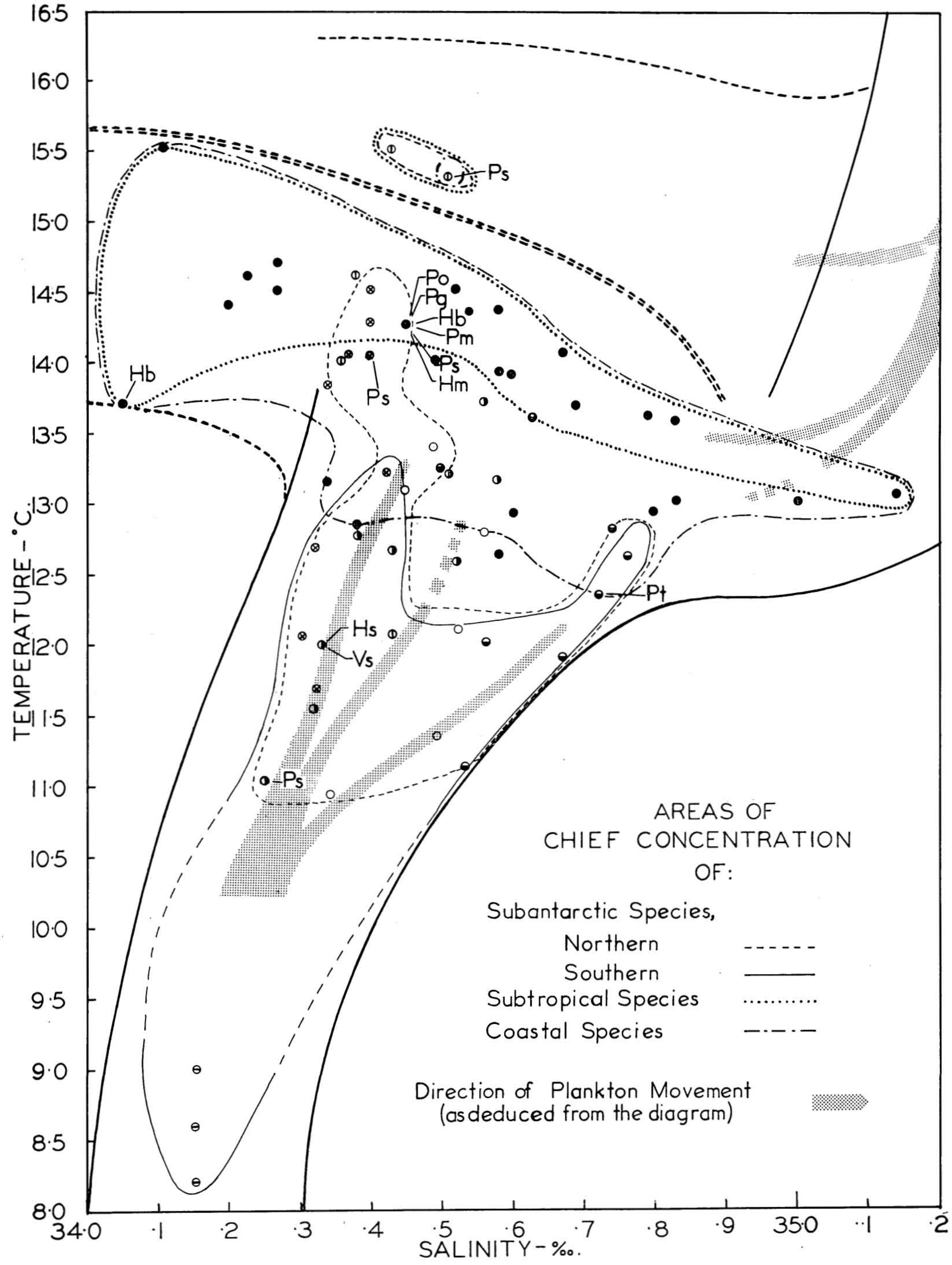


FIG. 2. Generalised T–S–P diagram showing areas of chief concentration of indicator groups of species for waters of subtropical and subantarctic origins and for coastal waters. Species captured rarely are shown by their initial letters adjacent to the station at which they were captured (see text for Station 79). *Po* = *Platyscelis ovoides*. *Pg* = *Paralycaea gracilis*. *Hb* = *Hyperia bengalensis*. *Pm* = *Primno macropa*. *Ps* = *Phronima sedentaria*. *Hm* = *Hyperoche medusarum*. *Pt* = *Parascelis typhoides* (?). *Hs* = *Hyperia spinigera*. *Vs* = *Vibilia stebbingi* (?).

The species discussed normally inhabit waters of a restricted and specified range of properties. However, the subantarctic species *Parathemisto gaudichaudii* and *Cyllopus* spp. and the Coastal species *P. australis* and *P. gracilipes* occur together at Stations 308, 292, 330, 310, 279, and again at Station 189 (Figs. 1, 2); again, the subtropical species *Hyperoche mediterranea* and the coastal species *P. australis* and *P. gracilipes* occur at Station 79. These collections of amphipods of mixed origin are present along with other species belonging to one or more of the several indicator groups of species. This is interpreted as evidence that the waters in which the species are habitually present are mixing together.

The water movements in the area have been deduced from the combined evidence of distributions of salinities, temperatures, and the zooplanktonic indicator species. They are discussed in detail elsewhere (Bary, 1959), but the isotherms of Figures 5 and 6 serve as a basis to recapitulate the main features. Briefly, there appears to be a moderately strong influence from water of subtropical origin which extends from the west into Foveaux Strait and can be traced around the coast to Dunedin and beyond. It is probable that some water of subantarctic origin, mixed with the subtropical water, also enters the Strait from the west. Water of subantarctic origin periodically penetrates in smaller or larger intrusions into the waters in the Strait and coastal areas. These several waters mix to form one of intermediate properties which is designated herein as "coastal water" (Fig. 1). It is believed probable that only water of subantarctic origin is present at Stations 826 and 921 of Series 7, and possibly also at Station 725 (Figs. 1, 6*c*). Data from stations of Series 5 and 6 (Fig. 6), together with those from a surface thermograph trace made two weeks later, on a course parallel to and seaward of the stations of Series 6, indicate the location of the subtropical convergence. It was not crossed by "Lachlan" in January when it was probably to the north of Station 1, but it was present a little northward of Station 330 in March (Series 6).

With the species of Amphipoda related to their respective waters by the T–S–P diagrams, their presence or absence at a station becomes significant in that there is an indication of the waters present. The subtropical species *Hyperoche mediterranea* is confined to that portion of Foveaux Strait likely to be most directly influenced by water of subtropical origin (Fig. 5*a*). The coastal species *Parathemisto australis* and *P. gracilipes* occur along with *H. mediterranea*, but in all series they occur over a larger area, and a wider range of temperatures. From Figure 5*a* to *d*, it is clear that neither subtropical nor coastal species penetrate into areas where the influence of water of subantarctic origin is strong, e.g., Stations 210 to 218 (Fig. 5*c*, *g*), or 285, 297 (Fig. 5*d*, *h*). On the other hand they are found, together with subantarctic species, at those stations in the mixed waters immediately northeast of Stewart Island (Fig. 5*a*, *e*) and more especially at Stations 187, 189 (Fig. 5*b*, *f*), 208 (Fig. 5*c*, *g*), 279, 292, 308, 310 (Fig. 5*d*, *h*), and again at Station 330 (Fig. 6*d*, *e*). In the T–S diagram (Fig. 1) these stations (except 187, 189) are seen to extend as a group between water of subantarctic origin and coastal water. In the T–S–P diagrams Figures 2, 3 the occurrence of the subantarctic species of plankton at all of these stations emphasises a certain affinity between them; it would seem that they are directly within the influence of water of subantarctic origin. This is confirmed by the geographic charts, which suggest that although some of the stations are located in inshore waters each, in fact, is located in the vicinity of tongues of colder water penetrating shorewards. This is especially so for Stations 279 and 292, less so for Station 208. Stations 308 and 310 appear to be in waters that are more generally mixed, but into which water of subantarctic origin appears to be intruding, particularly about Station 297 (Fig. 5*d*, *h*). Stations 187 and 189 (Fig. 5*b*, *f*) are also located near intruding

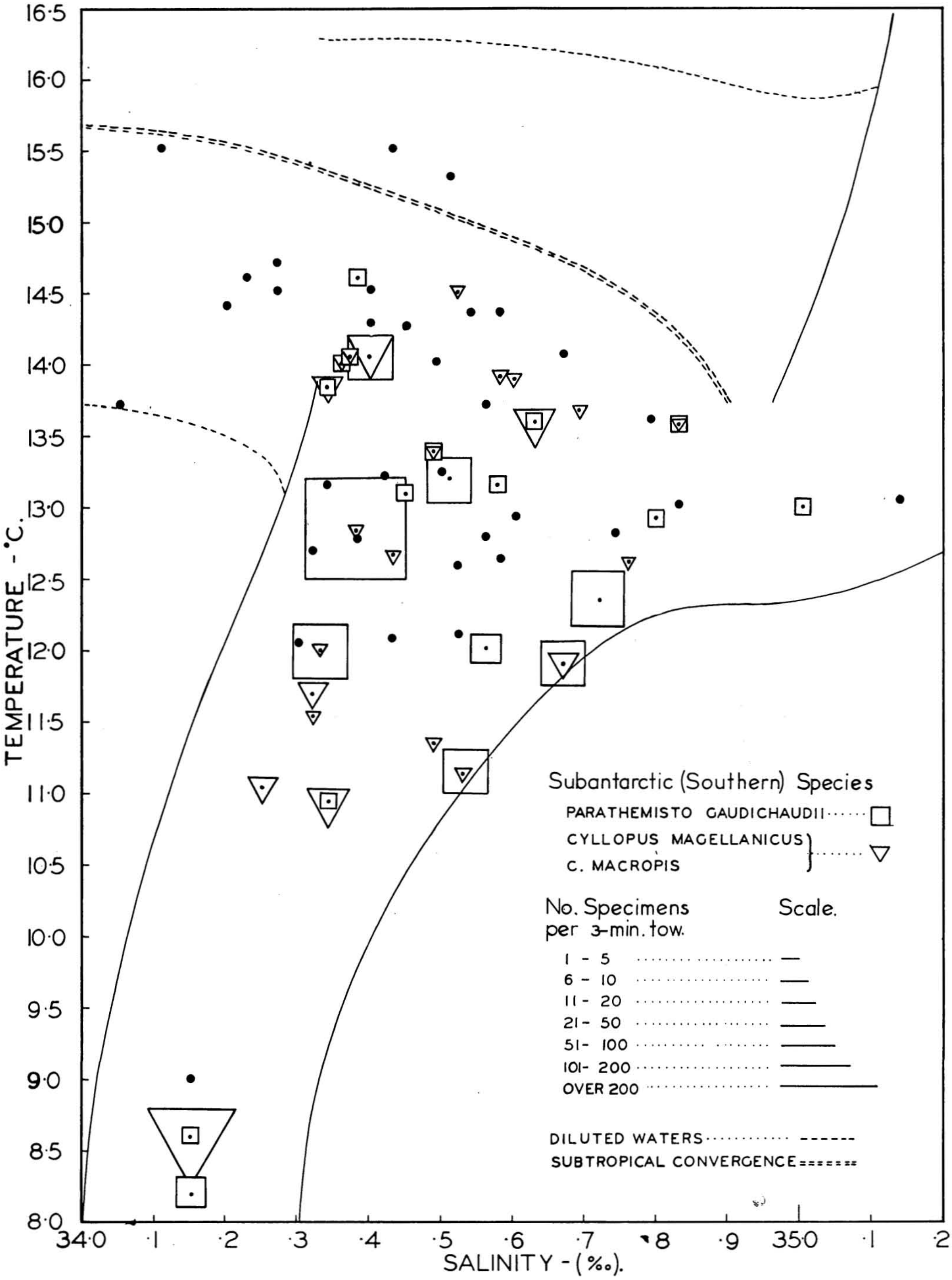


FIG. 3. Temperature–salinity–plankton (T–S–P) diagram of the species of Amphipoda associated with water of subantarctic origin.

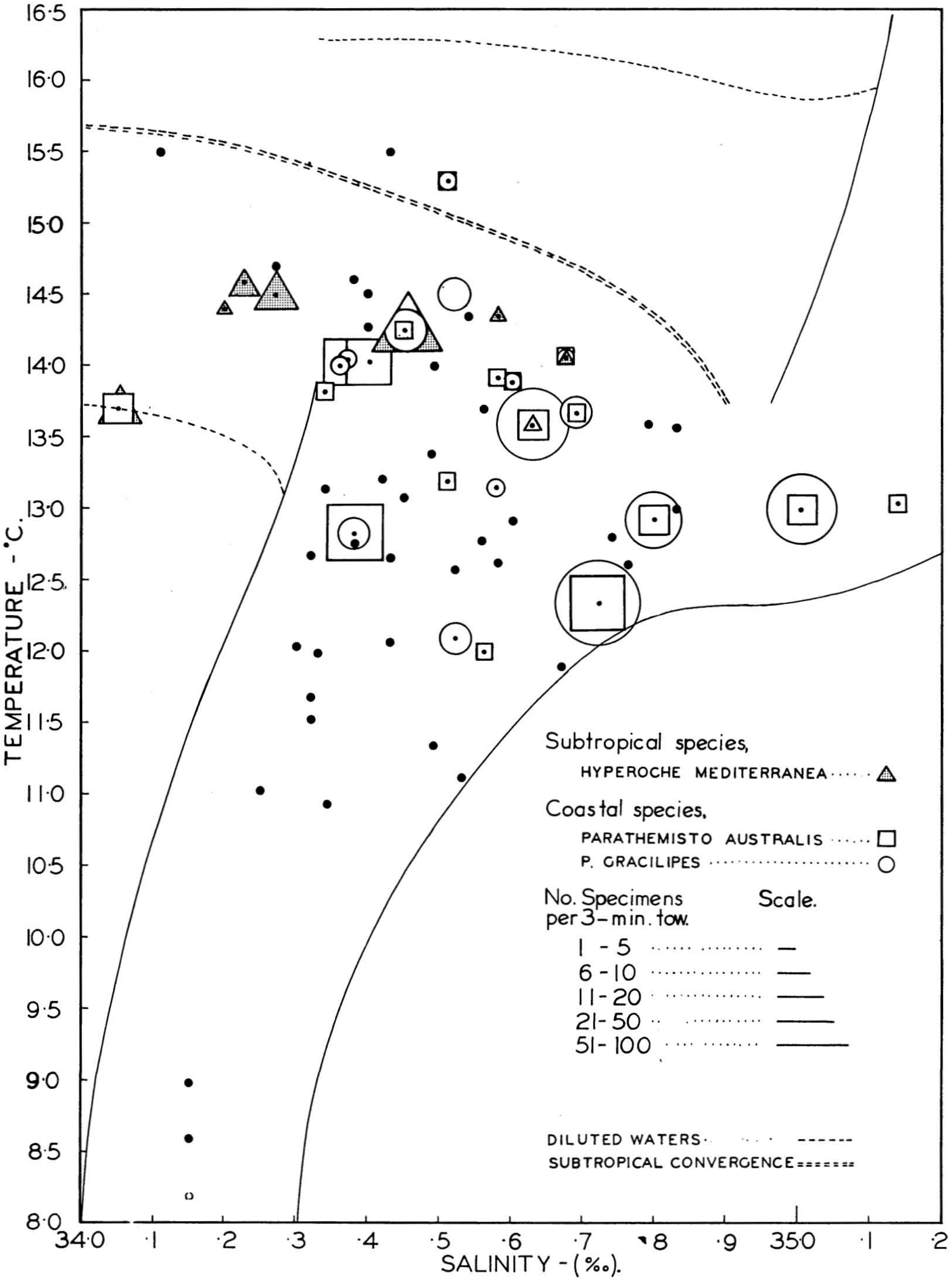


FIG. 4. T–S–P diagram of the species of Amphipoda associated with water of subtropical origin, and with co ıstal waters.

subantarctic water, and again the mixture of species results. At these stations there is a slightly stronger influence of coastal water than in the previous examples, as shown by higher salinities (Fig. 1). The absence of any subtropical species at 187 and 189 suggests little influence from water of this source.

The isotherms for January (Series 5, Fig. 6*a*, *b*) indicate that water of subantarctic origin extends at least to Cook Strait. One or both of the subantarctic species *Parathemisto gaudichaudii* and *Cyllopus magellanicus* are present at four of the six stations. They are absent from Stations 3 and 4. This, together with salinities which are a little higher than in neighbouring subantarctic water (Fig. 1), indicates that those stations are being influenced by coastal water, probably from south of Banks Peninsula. Although this water does not exclude subantarctic species, it supplies a reason as to why *Parathemisto gracilipes* occurs at Station 3 (and also why other species of the Coastal Group were present at both Stations 3 and 4). In Figure 6*d*, *e*, the subtropical convergence transects the series. Subantarctic species are present at Stations 337 and 330; *P. gracilipes* is also present at Station 330, and both *P. gracilipes* and *P. australis* at 322. Station 322, north of the convergence, is in mixed subtropical-coastal waters (Figs. 1, 2) and the occurrence there of a coastal species is consistent. Species from all groups are to be expected at Station 330. It is shown by the mixture of zooplankton to be situated in mixing waters in the T–S–P diagram (Fig. 2), and this is borne out by its geographical location near or within the mixing area between waters originating in the subtropical and subantarctic masses (Fig. 6*d*, *e*).

Perhaps the most important feature illustrated by Figure 6 is that the two subantarctic species, few in individuals though they are, are present only in water believed to have originated in the subantarctic. They act as indicators and demonstrate the northward extent of subantarctic water, as well as demarcate the approximate position of the subtropical convergence in March, 1951.

It perhaps should be emphasised at this point that in the southeast coastal area of New Zealand, where mixed waters of diverse origins predominate, it would be most difficult to disentangle the sources of the waters and the species from charts of distributions alone. Interpretations would be largely deductive and subjective. The T–S–P diagram demonstrates in a clear and effective manner, the source of both the waters and the species in the area. At the same time it provides a means of utilising occurrences of species to follow the trends of water movements. Thus the occurrences of species of plankton at certain localities, and of the means by which they arrived at their point of capture, can be explained with a fair degree of certainty.

Rare species are symbolised in Figures 2, 5, and 6 by their initial letters. Occurrences of one or a few species, on one or two occasions, are often insignificant in distributional studies. In the context of the T–S–P diagram (Fig. 2), however, their occurrences may assist in the interpretation of conditions; conversely, the conditions in which they occur may assist in interpreting other features concerning the species, e.g., see a later discussion of *Parathemisto* spp.

The cold-water species *Hyperia spinigera* is demonstrated as being captured in water of subantarctic origin (Station 210, Figs. 2, 5*g*)—water in which the species is normally resident. *Hyperoche medusarum* Kroyer, another cold-water species, occurs at Station 79 (Figs. 2, 5*a*). This might be regarded as a stray specimen, but the presence of small numbers of other species of the Subantarctic groups, e.g., Copepoda, suggests an intrusion of water of subantarctic origin towards this station. Two species present at Station 79 are of subtropical origin, namely *Platyscelus ovoides* (Claus) and *Paralycaea gracilis* Claus. These, and probably also *Hyperia bengalensis*, are regarded as entering, along with water of subtropical origin, into Foveaux Strait from the west. As would be expected, undoubted cos-

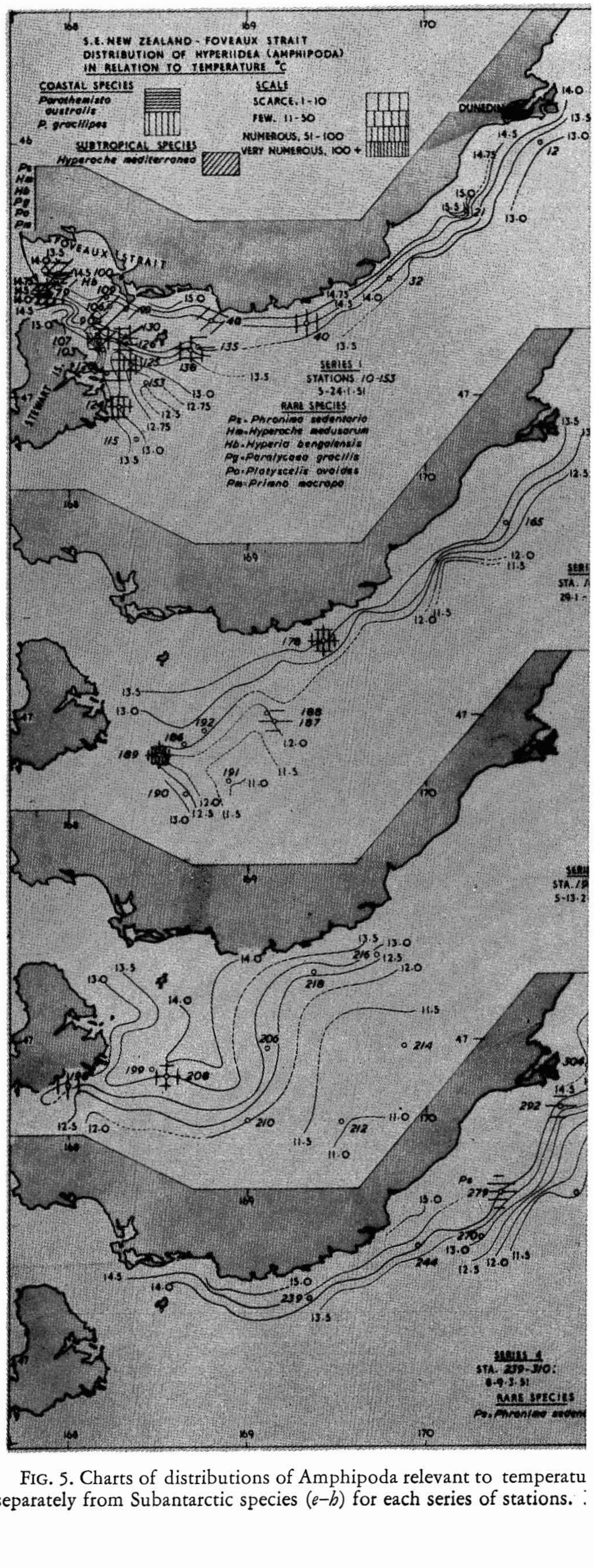


FIG. 5. Charts of distributions of Amphipoda relevant to temperatu
separately from Subantarctic species (*e–h*) for each series of stations.

mopolites may occur at stations located in a variety of waters. Thus, *Phronima sedentaria* (Forskal) is present in water of subtropical origin north of the subtropical convergence (Station 326, Figs. 2, 6*d*), in mixed water (Station 79, Fig. 5*a*), and in water predominantly of subantarctic origin (Stations 214, Fig. 5*g*), or being influenced by this water (Station 279, Fig. 5*h*). *Hyperia bengalensis* (Giles) was present in mixed or diluted coastal waters (Stations 79, 100), and *Primno macropa* Guer., another cosmopolitan species, also occurred at Station 79 (Figs. 2, 5*a*). Thus, on the whole, these species are shown to have been captured in conditions suitable for them. Conversely, their occurrences in conditions consistent with those previously recorded for them adds to the value of interpretations based on the more commonly occurring species.

Two of the New Zealand species listed in Table 1 are regarded as being doubtfully identified (Hurley, 1955). The identification of one, and possibly also of the other species, is not upheld when their relationships to the water masses, demonstrated in the T–S–P diagram, are compared with their previously recorded distributions. *Vibilia stebbingi* (?) Behn and Wolt, is present in water of subantarctic origin (Station 210, Figs. 2, 5*g*) which is out of character with the tropical-subtropical range usually ascribed to this species. *Parascelis typhoides* (?) Claus, another tropical-subtropical species was captured at Station 189 (Figs. 2, 5*f*), believed to be located in a mixture of coastal and subantarctic waters; the absence of any others of the selected Subtropical Group of species indicates little influence at this point from water of subtropical origin. Thus this occurrence of *P. typhoides* (?) may also be anomalous, suggesting again that misidentification is possible.

A comparison of the average numbers of a species captured in coastal and in offshore waters may indicate the degree to which the species penetrate from one water into the other. When numbers captured per haul over a specified range of depth are plotted against depth of water, the commoner amphipod species illustrate that this applies. (See Fig. 7; deeper water in the area of sampling is indicative of an increase of distance offshore and proximity to oceanic water.)

Both *P. gaudichaudii* and *Cyllopus magellanicus* (Fig. 8, unbroken line) show decided increases in the numbers captured from shallow (coastal) to deep water. A fair degree of tolerance to coastal waters is suggested for *P. gaudichaudii* by the almost steady increase in numbers as samples proceed offshore. On the other hand, the sudden decrease in water shallower than 50 fathoms (91.5 m.) shown by *C. magellanicus* is indicative of intolerance to conditions in the coastal water. *P. gracilipes* and *P. australis* (Fig. 7) increase in numbers to a peak at 50 fathoms (91.5 m.), and decrease in the deeper, offshore water. This suggests that neither species is tolerant of conditions in this water (see later). These facts confirm the relationships of the species to water masses already obtained from the T–S–P diagrams (Figs. 2, 3, 4).

The collections of this study were made during a period of three months. During the latter half of this a larger proportion of stations were over deeper water, either directly influenced by, or believed to be situated in water of subantarctic origin. It seemed possible, therefore, that variations in the catches of a species, relative to depth of water, might be reflected in the numbers captured at different times in the three months. So that direct comparisons might be made, the average number of specimens per haul for each month are included in the figures of changes of the catch with depth (Fig. 7 dashed line). *Cyllopus magellanicus* shows an overall decrease in numbers during January through March which is opposed to the increase with depth. Numbers of *P. gaudichaudii* on the other hand, increase with each monthly catch, although less so for March than for January and February. Even so, the number collected

TABLE 1

RARELY CAPTURED SPECIES AND THEIR PREVIOUSLY RECORDED DISTRIBUTION IN RELATION TO THAT SHOWN BY THE T–S–P DIAGRAM

SPECIES	SYMBOLS IN FIGURES	STATIONS COLLECTED	NUMBER OF SPECIMENS	DISTRIBUTION		AS FROM T–S–P	AGREEMENT
				Recorded in literature	Summary*		
1. *Vibilia stebbingi ?*	Vs	210	1	Mediterranean; 35°N.–30°S. Atlantic; E. Pacific; N.Z.	ST–T	SA	Poor (possibly misidentified)
2. *Hyperia bengalensis*	Hb	83 100	14 4	40°N.–45°S. Atlantic; Mediterranean; Arabian Sea; Cape Howe and N.S.W., Australia; Bermuda	ST–COS	Mixed ST–C–SA	Satisfactory
3. *Hyperia spinigera*	Hs	210	1	North Norway; Labrador current; W. Ireland; S. England; E. mid-Atlantic; S. Georgia; Friday Harbour; N.Z.	Arctic–Subarctic; A–SA	SA	Very good
4. *Hyperoche medusarum*	Hm	75	1	55°–77°N. Atlantic; N. Alaska; S. Georgia; at 1500–3000 m., 19°–35°S. Atlantic; N.Z.	Arctic–Subarctic	Mixed ST–C–SA	Fair
5. *Phronima sedentaria*	Ps	82 214 279 326	1 1 3 1	Mediterranean; 60°N.–36°S. Atlantic; Indo-Pacific; N.Z.	COS	82 Mixed ST–C–SA 214 } SA 279 } SA 326 ST	Very good
6. *Primno macropa*	Pm	74 75	1 1	Mediterranean; 30°N.–66°S. Atlantic; Indian; N. Pacific; 58°–66°S. Pacific	COS	Mixed ST–C–SA	Good
7. *Paralycaea gracilis*	Pg	83	1	Mediterranean; 53°N., 47°N., and Trop. Atlantic; 39°S., 140°E., Pacific; N.Z.	T–ST	Mixed ST–C–SA	Satisfactory
8. *Parascelis typhoides ?*	Pt	189	1	N.–S. Atlantic; Mediterranean, Red Sea	T–ST	Mixed SA–C	Poor (possibly misidentified)
9. *Platyscelis ovoides*	Po	75	3	N.–S. Atlantic; Indian Ocean and G. of Aden; Mediterannean	T–ST	Mixed ST–C–SA	Fair

* T—Tropical; ST—Subtropical; SA—Subantarctic; A—Antarctic; COS—Cosmopolitan; C—Coastal.

per haul over 100 fathoms (182.9 m.) of water increases slightly. Captures of both *P. australis* and *P. gracilipes* increase to February and decrease to March. The T–S–P diagram demonstrates, however, that the two species are resident in coastal water, and it is probable therefore that the February-March (seasonal) decrease is not more than a contributing factor to the lower number of specimens captured from the deeper water. Thus, for the most part there appears to be a considerable degree of independence between the numbers of a species captured per haul per month and the numbers captured relative to depth of water. A similar condition is also suggested by the averages of all the common amphipods (Fig. 7). The average catch increases to 100 fathoms in a similar manner to that for January and February. However, the catch from water deeper than 100 fathoms continues to increase, although at a lesser rate, while the catch for March drops sharply.

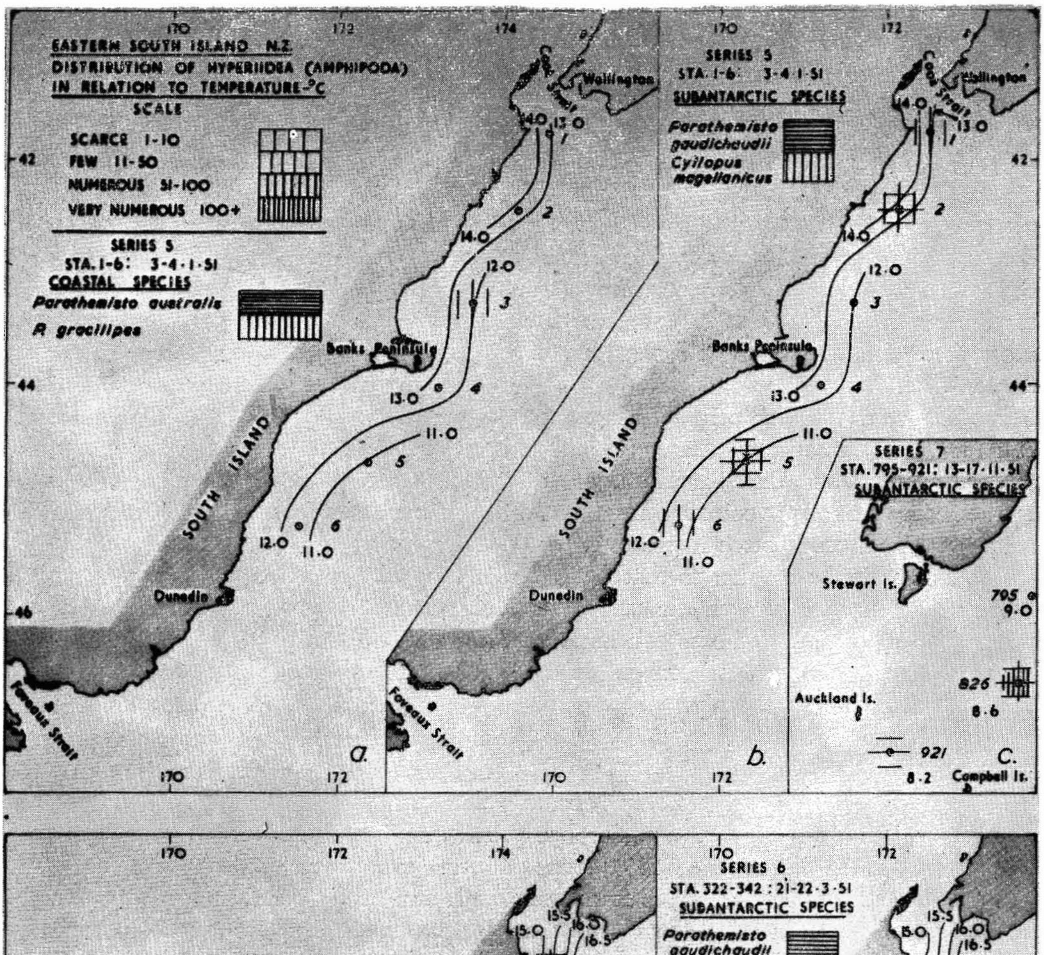
DIURNAL VARIATION

Vertical migration undoubtedly occurs among species of Amphipoda (e.g., Stephensen, 1925; Hardy and Gunther, 1935; Bousfield, 1951). However, other factors than light intensity would appear to be operative in the control of vertical distribution. Bousfield suggests quality and quantity of food, age of specimens and predation, and implies that the results of vertical migration may be modified by these. There may be vertical migration in connection with propagation as well (Stephensen). Stephensen also discusses the point that a number of species occur singly, or in groups of a few specimens. He considers that this applies to almost all deep-sea species, and also to some surface species. As well, there appears to be an inherent tendency for some species to shoal (Hardy and Gunther, 1935).

These several factors, some of which appear to be interrelated, almost inevitably would result in anomalous occurrences in terms of a normal diurnal rhythm. With species tending to appear somewhat irregularly at the surface, patchiness in their occurrences would result. Hardy and Gunther (1935) discuss such patchiness among amphipod species and the effects this has on their distribution patterns, with particular reference to the area about South Georgia.

The data on the species in the present study demonstrate that vertical migration takes place and that patchiness is frequently met. The former is reflected in diurnal variation of numbers at the surface, and the latter in the great variation in the numbers captured from hour to hour (Figs. 8, 9), or station to station, of all the common species (Figs. 5, 6). The average haul for each hour is derived from the average of one to five stations. In contrast the average number of tows per hour is low (almost three per hour), which precludes the present data from being fully representative of the patterns of diurnal variation in New Zealand waters.

However, the numbers of the five commonly captured species, and of the juveniles of *Parathemisto* spp., increased at night. *Parathemisto gaudichaudii* and juveniles of *Parathemisto* spp. exhibited pre- and post-midnight increases in numbers; although such is more or less typical of the diurnal behaviour of zooplankton (Cushing, 1951), the post-midnight rise occurs between 0100–0200 hours, which in southern New Zealand is several hours too early to be considered a predawn rise. The other species increase to a single peak during darkness either prior to (*Hyperoche mediterranea*), or subsequent to midnight (*Cyllopus magellanicus*, *Parathemisto australis*, *P. gracilipes* and *Parathemisto* juv.). A large catch of several species, made at Station 189 at 0125 hours, is responsible for the peak of numbers taken between 0100 and 0200 hours for *P. gaudichaudii*, *P. australis*, *P. gracilipes*, and *Parathemisto* juveniles. A total of four stations were occupied between 0100 and 0200 hours, but only at Station 189 were any of these species captured. This may be a result of patchiness in distribution. On the other hand, Station 189 was in mixed coastal-subantarctic


EASTERN SOUTH ISLAND N.Z.
DISTRIBUTION OF HYPERIIDEA (AMPHIPODA)
IN RELATION TO TEMPERATURE-°C
SCALE
SCARCE 1-10
FEW 11-50
NUMEROUS 51-100
VERY NUMEROUS 100+
SERIES 5
STA. 1-6: 3-4-1-51
COASTAL SPECIES
Parathemisto australis
P. gracilipes
Wellington
Banks Peninsula
SOUTH ISLAND
Dunedin
Foveaux Strait
a.
SERIES 5
STA. 1-6: 3-4-1-51
SUBANTARCTIC SPECIES
Parathemisto gaudichaudii
Cyllopus magellanicus
b.
SERIES 7
STA. 795-921: 13-17-11-51
SUBANTARCTIC SPECIES
Stewart Is.
Auckland Is.
Campbell Is.
c.
SERIES 6
STA. 322-342: 21-22-3-51
COASTAL SPECIES
Parathemisto australis
P. gracilipes
RARE SPECIES
Ps = Phronima sedentaria
d.
SERIES 6
STA. 322-342 : 21-22-3-51
SUBANTARCTIC SPECIES
Parathemisto gaudichaudii
Cyllopus magellanicus
e.
SERIES 7
STA. 795-826: 13-17-11-51
Stewart Is.
COASTAL & SUBTROPICAL SPECIES---NIL
Auckland Is.
Campbell Is.
f.

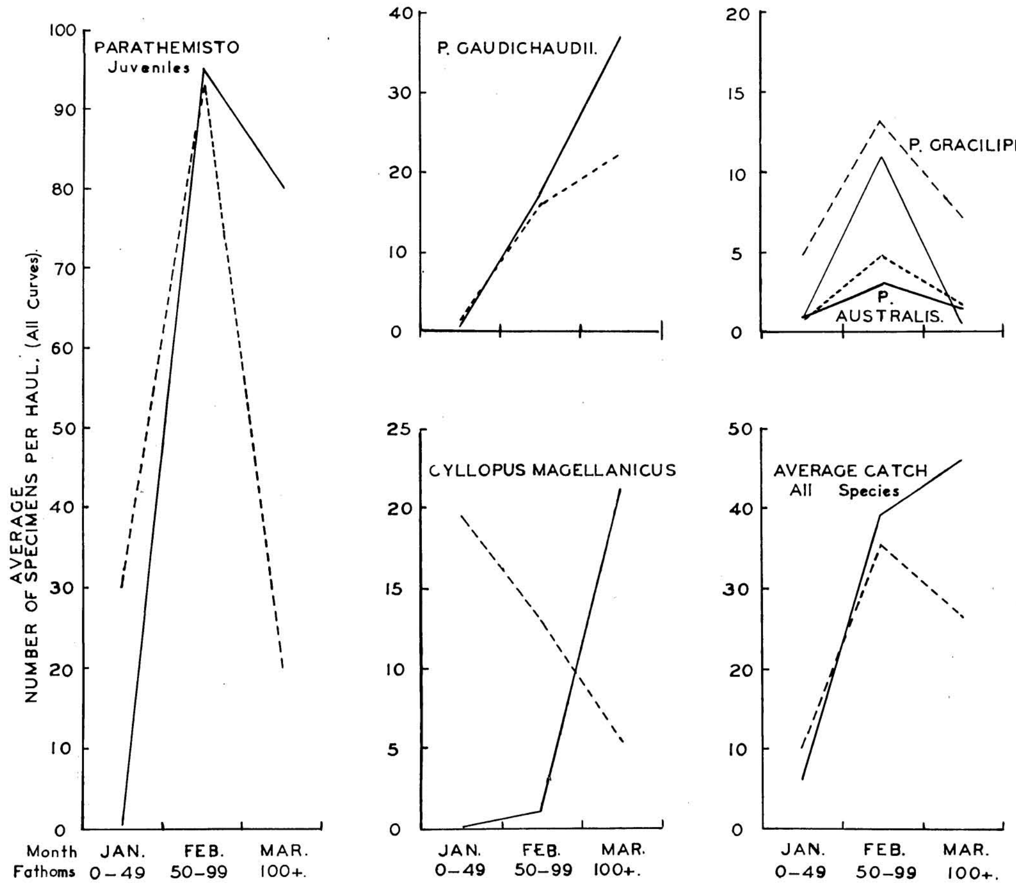


FIG. 7. The average number of the commonly occurring Amphipoda per haul per month for January, February, and March, plotted together with the average number of species per haul over each of the ranges of depth 0–49, 50–99 and 100+ fathoms (0–89.6, 91.4–181.1, and 182.9+ m.).

waters and perhaps the several species were dependent on the particular hydrological conditions. That these examples of diurnal variation are so weighted by a single haul indicates the need for a large number of samples when dealing with species exhibiting such variable distributions in time.

Several quite considerable hauls made in daylight (Figs. 8, 9) emphasise what appears to be a certain independence of controlling conditions (e.g., light intensity) in the vertical movements of the several species. Daylight hauls were scattered over a range of conditions (see Fig. 1) and thus it is unlikely that too frequent sampling in particularly favourable conditions is weighting the curves. *Parathemisto gracilipes* and *P. australis* (Fig. 8) were most consistently present in daylight, the one or the other being captured at most times. *P. gaudichaudii*, *Parathemisto* juveniles, *Cyllopus magellanicus*, and *Hyperoche mediterranea* were usually taken in very small numbers during daylight (Fig. 8). It seems probable from the 2-hour averages of all spe-

FIG. 6. Charts of distributions of Amphipoda relevant to temperature for the east coast of South Island. Coastal species (*a–c*) are shown separately from Subantarctic species (*d–f*) for stations of Series 5 and 6.

cies (Fig. 9) that species may be present, in moderate numbers, up to midmorning and from midafternoon on. However, all species, except *P. gracilipes* and a few *P. australis*, were absent or rarely captured in hauls between these times.

The common species of amphipod, by their irregular, spasmodic occurrences, suggest that in New Zealand waters, as elsewhere, distribution is affected by patchiness, and that a degree of independence of known controlling factors in the vertical movements of species is probable. Interpretations of distributions of species may thus be conditioned by the presence or absence of specimens as a result of (undetected) irregularities in their vertical movements.

PARATHEMISTO SPECIES

Hurley (1955) analyses the complex taxonomy of *P. gaudichaudii*, *P. australis*, and *P. gracilipes*. He points out (p. 161) that "although the three groups of *Parathemisto* here recorded from New Zealand can be separated quite distinctly by the pectination of the uropods, the general facies and by ecological preferences and habits, it is still possible that they do not warrant specific status. . . ." He briefly discusses the ecological data available to him from preliminary studies, and their relationships to the systematic positions of the species. As a result of the more detailed treatment possible in the present study, Hurley's general statement can now be amplified and modified.

In the preliminary studies it appeared that the habitats of *P. australis* and *P. gracilipes*, although overlapping, were separable respectively into shallow inshore waters and waters of intermediate depth. However, the T–S–P diagram (Fig. 4) shows that they occur at similar temperatures and salinities frequently at the same stations, in the warm coastal and mixed waters. In contrast, *P. gaudichaudii* inhabits colder water originating in the subantarctic, although it is able to penetrate into the inshore waters. Thus, for the area in question, there appear to be environmental preferences between *P. gaudichaudii* on the one hand and *P. gracilipes* and *P. australis* on the other, but not between *P. gracilipes* and *P. australis*, which facts are well demonstrated in the T–S–P diagrams (Figs. 3, 4).

The variations in the diurnal patterns of the three species provide further evidence toward distinguishing between *P. gaudichaudii* and *P. australis–P. gracilipes*. *P. gaudichaudii* is rarely taken at the surface during daylight, but *P. gracilipes* and *P. australis* may be common (Figs. 8, 9). There is a double peak of numbers for *P. gaudichaudii* during darkness; both *P. australis* and *P. gracilipes* occur in large numbers at one and the same time. Further, the curve of diurnal variation for *P. gracilipes* closely parallels that for *P. australis*, indicating similar reactions to changing conditions (Fig. 9). Other similarities between *P. gracilipes* and *P. australis* are apparent in their relations to depth of water, and in the increases and decreases in numbers during January through March (Fig. 7). *P. gaudichaudii* differs considerably on these two points.

Ecologically, it would appear that *Parathemisto gaudichaudii* is separable as a distinct species from *P. australis* and *P. gracilipes*. However, an ecological distinction between *P. australis* and *P. gracilipes* in the New Zealand area cannot be substantiated because of their closely parallel diurnal behaviour and similar distribution. These points are probably not of sufficient moment to make *P. gracilipes* and *P. australis* conspecific, especially as Hurley states the two forms are readily separable by their general facies. Their previous distributional records, too, indicate that the former is an oceanic, and the latter a coastal species. Although such markedly different distributions should be reflected in their relationships to water masses in T–S–P diagram, this is not so. Thus the ecology of *P. gracilipes* and *P. australis* does little to assist in clarifying their systematic positions. On balance, it seems, however, that some taxo-

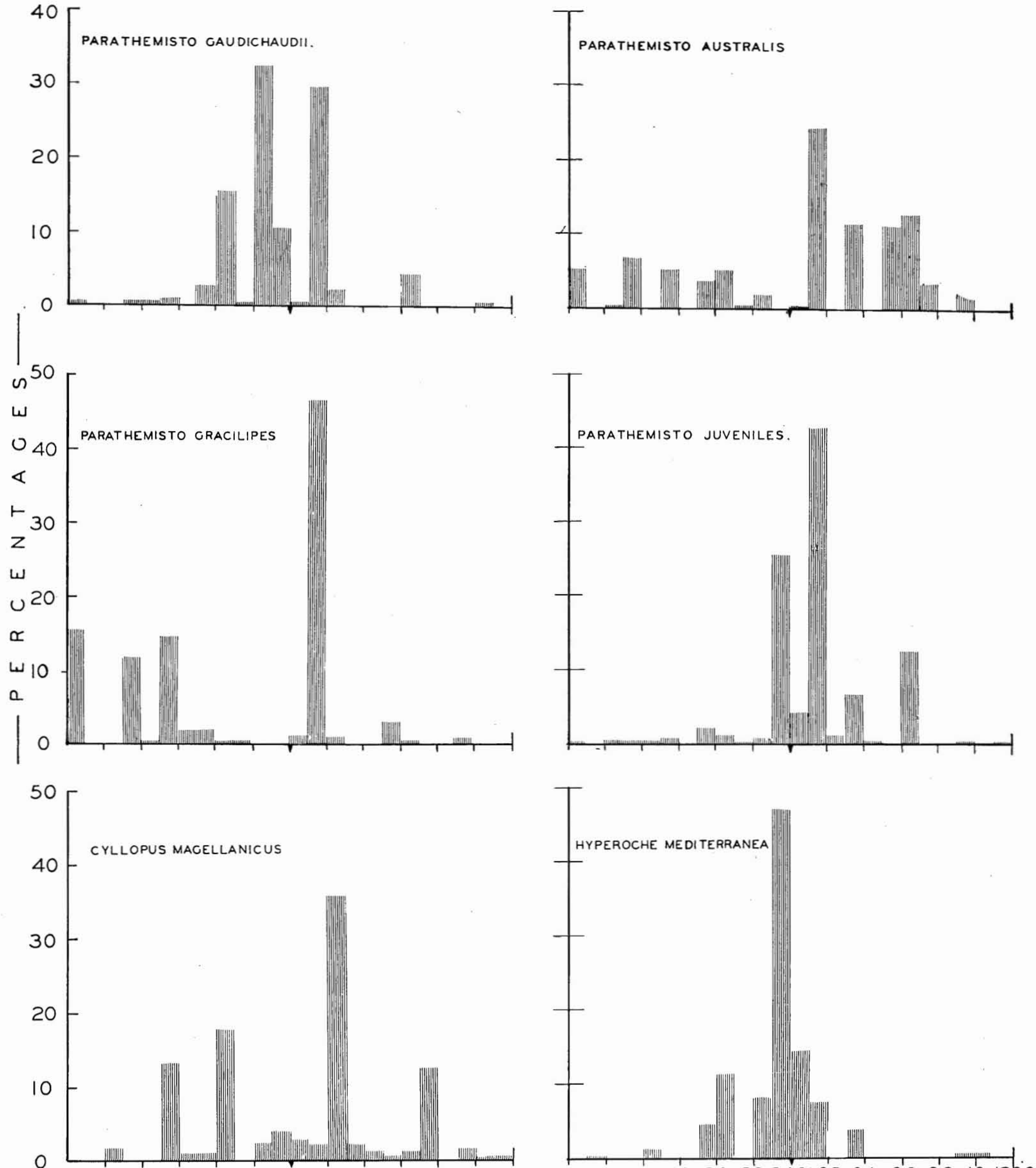


FIG. 8. The diurnal variation at the surface as shown by the hourly catches of commonly occurring species expressed as a percentage of the total catch of the species.

nomic distinction between them is desirable, but preferably at an infraspecific level.

AMPHIPODS IN THE ECONOMY OF THE AREA

An assessment of the position of species of Amphipoda in the productive economy of southern New Zealand waters was not aimed at, although the common species would seem to be important. Species are frequently captured and may occur in large numbers, even in the 3-minute tow, e.g., 729 *P. gaudichaudii* collected from 22 stations; 408 *P. gracilipes*

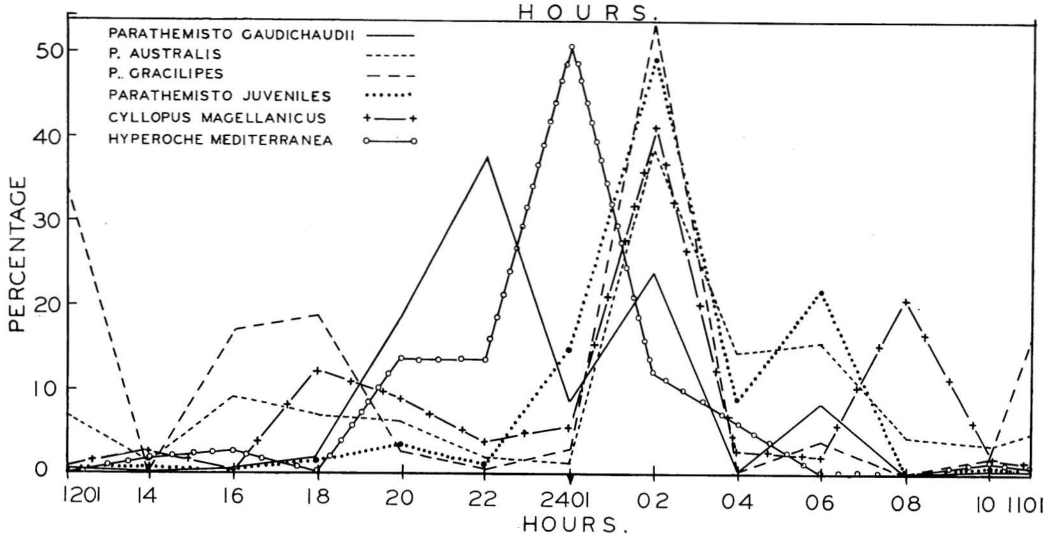


FIG. 9. The diurnal variation as shown by 2-hour averages of the data in Figure 8.

from 18 stations; 3,500 *Parathemisto* juveniles from 32 stations. The numbers of juveniles captured decrease rapidly between February and March (Fig. 7) but, even so, they were present in fairly high numbers throughout the summer. They ranged in size between specimens just released from the brood pouch to about 6.5 mm. long (at which length they usually can be assigned to sex and species), and because of their numbers are probably important in food cycles.

Barnard (1930) noted an increase in the sizes of the adults of Amphipoda at higher latitudes. In the present material, specimens of *Cyllopus magellanicus*, captured in the warmed waters (12–13°C.) of subantarctic origin off the New Zealand coast, averaged 7 to 8 mm. long and only occasionally exceeded 9 mm.; those from Station 826 (Fig. 6), in colder water (8.6°C.), averaged 9 to 10 mm. and were often 11 mm. and longer. If numbers of a species were maintained in the colder waters, such an increase in size would be reflected in an increased bulk of material available as food. Thus the size-increase in southern waters may well be related to production, the more so if it is a widespread phenomenon among those dominant species of the zooplankton.

Except for juvenile stages, the numbers of the species of amphipods captured do not reach those of some euphausiids or copepods in the area, but their large size and frequent occurrence in both oceanic and coastal waters (together with the fact that oceanic species may extend into coastal waters), suggest that species are important in productivity throughout the area. This is in part borne out by the quantities of these and other species of amphipod which are often present in the stomach contents of birds (e.g., Dawbin, 1954), and by personal observations of *Puffinus griseus* (flocks of which reach many thousands of birds) and of fish stomachs.

DISCUSSION AND SUMMARY

Of the 14 species of hyperiid Amphipoda collected by the "Lachlan" between Wellington and Auckland-Campbell islands, five are sufficiently common to be of value in studies of distribution. The occurrences of these and the remaining nine species are of interest when considered in relation to the water properties from which they were taken. In general, a strong affinity to the subantarctic, and to a lesser extent the antarctic faunas, is indicated in the frequent occurrences of species typical of southern waters, viz., *Parathe-*

misto gaudichaudii and *Cyllopus magellanicus* (and also *C. macropis*). Two species, *Hyperia spinigera* and *Hyperoche medusarum*, were rarely captured, but may be considered as inhabitants of cold waters. In the New Zealand area the first occurred in water of subantarctic origin, the second in mixed water, probably being influenced by subantarctic water. The influence of subtropical water is apparent in the moderate numbers of *Hyperoche mediterranea*, a warm-water species captured in western Foveaux Strait. Additional evidence of this influence accrues from the rare occurrences of other warm-water species, *Platyscelis ovoides*, *Paralycaea gracilis*, and possibly also *Hyperia bengalensis*. The cosmopolitan species *Phronima sedentaria* and *Primno macropa* were in low numbers, but were present in mixed subtropical-coastal waters and also in water of subantarctic origin.

There is reasonably close agreement between the distributions of species relative to water properties in the area, as shown by the T–S–P diagrams, and their distributions as recorded previously. It is rare in these earlier accounts for temperatures and/or salinities to be included, the relationships of which are important to the interpretation of species' distributions; nor are the interrelationships of species necessarily discussed. Data relevant to these features are necessary in discussion of vertical distribution where waters of diverse origins may be more or less stratified, and in horizontal distribution where waters of different properties may be mixing. It appears of small value to record the presence of species without also obtaining hydrological data by means of which ecological and distributional relationships may be assessed. With these data collected, the T–S–P diagram offers a means of precisely summarising it and, at the same time, demonstrating some of these relationships. The diagrams also emphasise the need to include, at least, data on temperatures and salinities in any discussion of distribution.

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