

Notes on Ecology, Distribution, and Systematics of Pelagic Tunicata from New Zealand

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THE COPELATA AND CYCLOMYARIA appear to be the only groups among pelagic tunicates to have been directly reported on for New Zealand, the former by Garstang and Georgeson (1935) and the latter by Garstang (1933). These reports resulted from collections of the "Terra Nova" Expedition. Thompson (1948) in a comprehensive treatise on "Pelagic Tunicates of Australia" refers only occasionally to New Zealand species.

Samples were collected from H.M.N.Z.S. "Lachlan" (Bary, 1956) to the south and east of New Zealand. *Oikopleura fusiformis* was captured mainly from cooler oceanic waters and is a new record for New Zealand. *O. dioica* occurred infrequently in warm coastal waters. Gonozooids and phorozoids of *Doliolum* (*Dolioletta*) *valdiviae* were obtained, and the "old nurse" stage is believed to have been identified. The remaining two orders, Pyrosomida and Desmomyaria, were also represented. *Pyrosoma atlanticum* was very abundant, especially in March and April, and *P. spinosum* was collected once as an incomplete colony. Both are apparently new records for New Zealand, and, in the case of *P. spinosum*, for Australia and the South Pacific as well (Metcalf and Hopkins, 1919; Thompson, 1948; Sewell, 1953). Of the five species of Salpidae (O. Desmomyaria) collected *Iasis zonaria* was rare; *Thalia democratica* was present at a few stations, but in very large numbers; one specimen of *Pegea confoederata* was captured; *Salpa fusiformis* f. *aspera* was common, and *Iblea magalbanica* was very common.

MATERIALS AND METHODS

These have been detailed elsewhere (Bary, 1956, and 1959a, 1959b). Briefly, collections

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were made in near and offshore waters to the east and south of South Island, New Zealand (January to March, 1951) and southward to Auckland and Campbell islands (November, 1951) from H.M.N.Z.S. "Lachlan," a naval frigate on surveying duties. Tows, made predominantly in the surface layer (there were a few oblique tows), were of 3 minutes' duration at 1½ to 2 kt. with a net of 50 cm. diameter constructed with graded silks. Procedure was standardised and some quantitative analyses have been made. Surface temperatures were taken and salinities were determined for many of the plankton stations, and at other locations as well.

Temperature-Salinity-Plankton diagrams are again utilised (Bary, 1959a; 1959b) and they assist with the interpretation of the origins and distribution of species.

Previous Records from New Zealand

Four species of Copelata and four species of Cyclomyaria have been reported from the Terra Nova collections, made in the vicinity of Three Kings Islands, northern New Zealand. These are: *Oikopleura longicauda* Vogt, *O. rufescens* Fol, *O. dioica* Fol, *Stegosoma conogaster* Garstang and Georgeson, *Doliolum denticulatum* Quoy and Gaimard, *Dolioletta gegenbauri* Ulanin, *Doliolina mülleri* Krohn, and *Dolioletta mirabilis* (Korotneff).

Other species were collected by "Terra Nova" to the south of New Zealand. It is possible that these may extend northwards towards southern New Zealand either in subantarctic water or the deep Antarctic Intermediate water whence upwelling might bring them to the surface. These species and the regions from which they were collected are: *Oikopleura valdiviae*, from 64°–72° S., common; *Folia gigas*, Antarctic, rare; *Pelagopleura magna*, Antarctic (71° S.), rare; and *Doliolina intermedium* var. *resistibile* Neumann, Antarctic, rare. Thompson (1948)

records five of the Terra Nova species from southeastern Australian waters, namely, *O. rufescens*, *O. dioica*, *O. longicauda*, *Dolioletta gegenbauri*, and *Doliolum denticulatum*. Thus, of the eight species recorded from the vicinity of New Zealand, two, *D. mülleri* and *D. mirabilis*, have not been recorded from Australia. The remainder are widespread in tropical and subtropical waters, and are common to the two countries.

The majority of tows of this present survey were in water of subantarctic origin in which fewer species occur (Thompson, 1942, 1948). However, further investigations in this water and a survey to the north of the subtropical convergence could not fail to be rewarding.

OBSERVATIONS ON SYSTEMATICS OF SPECIES

There is a long list of published literature on the complex systematics of the pelagic tunicata, and the following are representative: Ritter (1905), Salps, Doliolids, and Pyrosoma; Ritter and Byxbee (1905), Salps, Appendicularia, Pyrosoma; Aida (1907), Copelata; Metcalf (1918), Salpidae; Metcalf and Hopkins (1919), Pyrosoma; Essenberg (1926a), Copelata; Garstang (1933), Doliolids; Garstang and Georgeon (1935), Copelata; Thompson (1948), Sewell (1953), Copelata, Pyrosoma, Salpidae, and Doliolida. For bibliographies on each group, see Thompson (1948) and Sewell (1953). In view of these extensive works only brief notes are provided for most species in the following account, and only that literature actually cited is appended to the species.

Class I: COPELATA

Family OIKOPLEURIDAE

Genus OIKOPLEURA Mertens

Oikopleura fusiformis Fol.

Oikopleura fusiformis Aida, 1907; Essenberg, 1926a; Tokioka, 1940; Thompson, 1948

Over 4,000 specimens were collected from 10 hauls between Station 921 (51° 41' S.) and the south of Cook Strait (43° 15' S.), in January, 1951.

Characteristic features of the species are the long, slender fusiform body (Fig. 1) with

straight, flat dorsal contour, and the long narrow tail without subchordal cells.

Specimens from four stations were measured and the data are presented in Table 1.

Sizes and ratios of the New Zealand specimens are similar to those given by, for example, Essenberg (1926a) for California, Russell and Colman (1935) for the Great Barrier Reef, and Thompson (1948) for southeast Australian waters (see Table 2).

Tokioka (1940: 2-3) briefly discusses and illustrates the considerable variability of shape in the blind-sac of the left stomach. Similar variations appear characteristic of this organ in the New Zealand material.

A feature of New Zealand specimens was the high proportion (in some catches all) of specimens without the oikoplast epithelium. Whether the epithelium usually is sloughed, along with the throwing off of the "house," when specimens are captured, is not made clear by Essenberg (1926b) in his discussion of the disintegration and decay of specimens. It is not invariably so, however, as on several occasions specimens without the house, but with the oikoplast epithelium intact, were collected.

Oikopleura dioica Fol.

Oikopleura dioica Aida, 1907; Essenberg, 1926a; Tokioka, 1940; Thompson, 1948

Specimens were collected from six stations, but occurrences were spasmodic. Stations 12, 21, 32, 40, and 48 (numbers collected were estimated) constituted a continuous series of catches in early January in coastal waters.

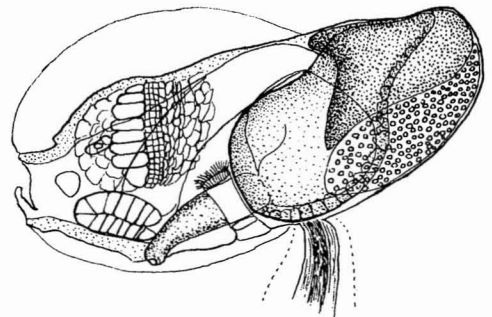


FIG. 1. *Oikopleura fusiformis*, a mature specimen of 0.9 mm. body length.

TABLE 1

THE RANGES AND THE RATIOS OF THE LENGTHS OF BODY AND TAIL OF *Oikopleura fusiformis* FROM NEW ZEALAND

STATION NO.	LENGTHS (MM.)				RATIOS, BODY TO TAIL		
	Body		Tail		Maximum	Minimum	Average
	Maximum	Minimum	Maximum	Minimum			
32	1.2	0.8	4.3	3.5	3.6	4.4	4.0
153	1.1	—	4.1	—	3.7	—	3.7
171	1.1	0.3	4.8	1.4	4.4	4.6	4.5
178	1.4	0.4	4.5	2.0	3.2	5.0	4.1
Averages					3.7	4.7	4.1

Oikopleura dioica (Fig. 2) is the only species so far described as being unisexual. This, together with a long tail with two subchordal cells, stout trunk, a characteristic posteroventral blind-sac to the right stomach, but absence of blind-sac on the left stomach, are features of diagnostic value (see Table 3).

Aida (1907) gives the body length of his largest specimen as 1111 μ , and the tail length as 3888 μ , i.e., a ratio of body to tail of 3.5; Essenberg (1926a) states that the body length ranges from 0.5 to over 1 mm., and that the tail is "about four times the length of the trunk." Thompson (1948) gives measurements of 0.3 to 1.2 mm. body length, 1.4–4.0 mm. tail length, the ratios of body to tail length being 4.7 and 3.3 respectively. Thus the New Zealand material corresponds well with that from elsewhere (excepting the ratio of 1:7.0 obtained for a small specimen with an abnormally long tail, captured at Station 12).

Class II: **ACOPA (CADUCICHORDATA)**
 Subclass **THALIACEAE**
 Order **PYROSOMIDA**
 Family **PYROSOMATIDAE**
 Genus **PYROSOMA** Peron

A detailed study of *Pyrosoma* by Metcalf and Hopkins (1919) is summarised and applied to Australian material by Thompson (1948). Sewell (1953) critically analyses these and other studies of the genus, and shows that many species and subspecies previously recognised are but growth stages of a relatively small number of species.

Two species were present in the New Zealand

material. One damaged specimen of *P. spinosum* was collected at Station 326; *P. atlanticum* occurred between Cook Strait and southern New Zealand, sometimes in very large numbers.

***Pyrosoma atlanticum* (Peron)**

Pyrosoma atlanticum Metcalf and Hopkins, 1919; Thompson, 1948; Sewell, 1953

Specimens from the tetrazooid to colonies 40 cm. long were present in moderate numbers, from the beginning of February. In March, and especially in April (collections partially

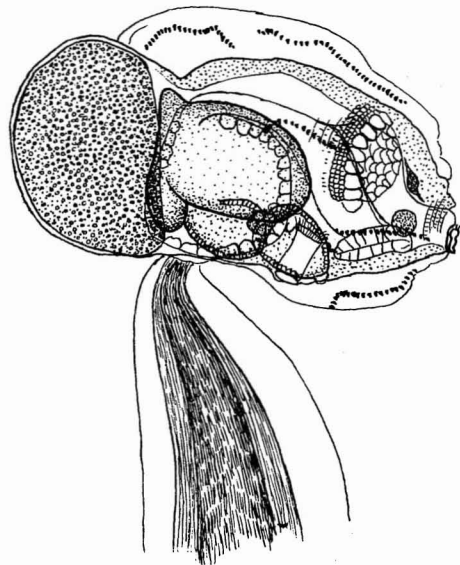


FIG. 2. *Oikopleura dioica*, a mature male of 1.1 mm. body length.

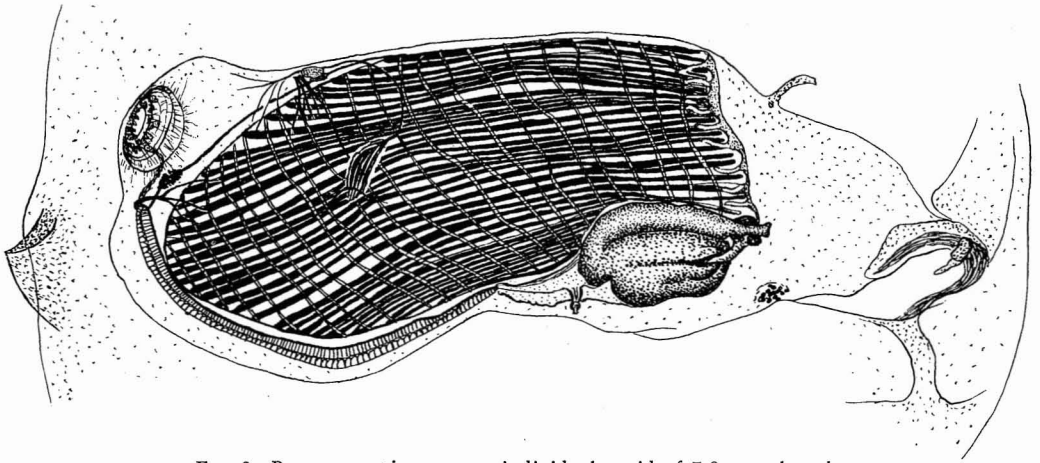


FIG. 3. *Pyrosoma spinosum*, an individual zooid of 7.0 mm. length.

analysed) very many thousands occurred off Dunedin and at several localities northwards of Dunedin.

In what proportions the *Pyrosoma* population should be divided between this, and the next species (*P. spinosum*) is not known. Thirty specimens, between the tetrazooid and large colonies, randomly selected from a number of samples, were closely examined and found to be *P. atlanticum*. And of many hundreds handled, only the one colony of *P. spinosum* was detected. *P. atlanticum* is therefore believed to predominate by a large majority.

Pyrosoma spinosum Herdman

Pyrosoma spinosum Herdman, 1888; Metcalf and Hopkins, 1919; Thompson, 1948; Berrill, 1950; Sewell, 1953

One colony secured at Station 326 constitutes a new record for New Zealand and Australia.

The zooid illustrated (Fig. 3) is 7 mm. extreme length. It possessed 23 gill bars, 35 rows of stigmata, and 9 languets, thus agreeing reasonably with numbers given by Sewell (1953) for a zooid of *P. spinosum* of 6.9 mm. (29–30 gill bars, 40 stigmata, and 6–8 languets). There is agreement with other accounts in respect of the position of the anterior light organs; in the number of atrial and cloacal tentacles and their positions; the ventrally split cloacal aperture; the dorsad curvature of the anterior part of the endostyle; in the posteriorly located languets; and in general shape and proportions.

Sewell discusses a "renniform body," originally reported by Metcalf and Hopkins (1919), and present in a sac situated in the test wall a little posteroventrally to the anus. From its similar location to the cyathozooid in *P. atlanticum* Sewell concludes this body is an early stage of a cyathozooid. He mentions that when this organ is present there is no trace of a testis.

A "renniform body" was not identified for certain in the New Zealand material. However, a small granular body appeared to be situated in the test wall, in the position described for the "renniform body." That this may have been Sewell's developing cyathozooid is suggested by this location, and the fact that no testis was present in the zooids examined.

Order CYCLOMYARIA

Family DOLIOLIDAE

Genus DOLIOLETTA Borgert

Dolioletta valdiviae Neumann

Dolioletta valdiviae Garstang, 1933

The majority of specimens were collected at Stations 74–85; a few occurred subsequently at Stations 109, 124, and 178.

GONOOZOID: Length, 2.0 to 8.2 mm. (Figs. 4, 5, 6).

There are 26 dorsal and 15 ventral lamellae in the gill septum. The dorsal septum extends from about M.3 $\frac{1}{3}$ to M.6, and occasionally to M.6 $\frac{1}{4}$; the ventral septum extends forward to M.5. M.6 is of normal width dorsally and

TABLE 2

THE RANGES AND THE RATIOS OF THE LENGTHS OF BODY AND TAIL RECORDED FOR *Oikopleura fusiformis* FROM ELSEWHERE IN THE PACIFIC OCEAN THAN NEW ZEALAND

AUTHOR	LENGTHS				RATIOS, BODY TO TAIL LENGTH		
	Body		Tail		Maximum	Minimum	Average
	Maximum	Minimum	Maximum	Minimum			
Thompson	1.4	0.4	5.0	2.0	3.6	5	4.3
Russell and Colman	—	—	—	—	—	—	4
Essenberg	1.1	0.75	3.8	3.7	3.4	5.1	4.25

laterally, but narrows appreciably ventrally. The intestine forms a loose dextral coil; the anus is usually in a median position, but may be displaced slightly dorsally and to the right; the anus and the coil of the intestine lie between M.6 and M.7. The testis is coiled; it commences near the ovary, situated posterodorsally to the coil of intestine, runs forward to about M.5¼ on the left side, then loops back and curves behind and above the intestine, ending towards the right side where it is usually slightly enlarged. The endostyle runs from M.2½ to M.4½–4¾. The nerve ganglion is situated at M.3⅓.

PHOROZOOID: Similar to the gonozooid in appearance and size (Fig. 7). It is without gonads and possesses a median posteroventral process between M.7 and M.8 which receives muscle slips from M.7.

Garstang (1933) suggests that *D. valdiviae* may be a form of *D. mirabilis* (Korotneff). He supports this with argument concerning developmental trends in the location of the testis and branchial septa relative to muscle bands.

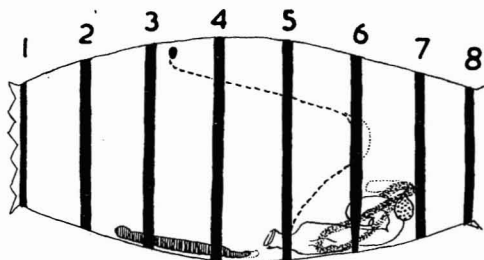


FIG. 4. *Doliolum (Dolioletta) valdiviae*, diagram of the gonozooid to illustrate the chief diagnostic features. M1 to M8, body muscles.

He says (p. 204) that "There is . . . a possibility . . . that the 'Specific' differences in the limiting attachments of the gill septum [between each of several pairs of species] are ultimately matters of differential growth rates and doubtless modifiable by nutrition, temperature, and similar environmental factors, as in other cases." Nevertheless he distinguishes *D. valdiviae* from *D. mirabilis* (= *cbuni*) by the different positions of attachment of the ventral septum and the extension behind M.6 of the septum, together with the length of the endostyle and the coiling of the testis (see Garstang, p. 216, fig. 5), and the fact that in *D. mirabilis* M.6 is incomplete ventrally, which is "without precedent" (p. 221). Sewell (1953: 53) regards the two gonozooids he collected as combining certain characters of both *D. valdiviae* and *D. mirabilis*: "In the length of the endostyle and the interrupted Vth body muscle, they conform to *D. mirabilis*, but the position and arrangement of the testis comes more nearly into line with the description of *D. valdiviae*. The ending of the gill lamella ventrally at the Vth muscle band agrees with *D. valdiviae*, whereas in *D. mirabilis* it is continued forward to the level of the IVth body muscle." He inclines to

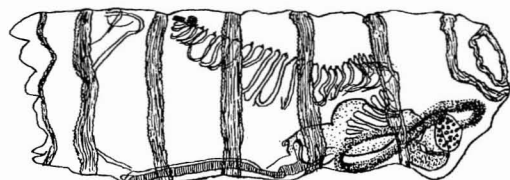


FIG. 5. *Doliolum (Dolioletta) valdiviae*, gonozooid of 3.9 mm. length.

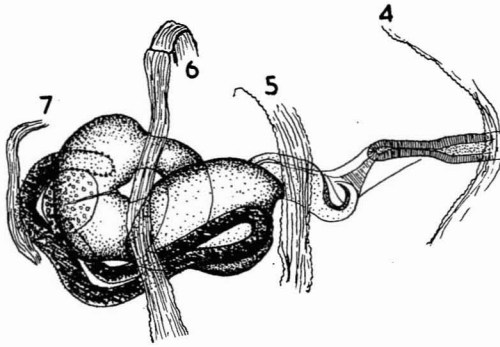


FIG. 6. *Doliioletta valdiviae*, ventral view of gut and gonads of gonozooid. M4 to M7, body muscles.

the belief that *D. valdiviae* may be a form of *D. mirabilis*.

From Sewell's account, it would seem that the "position and arrangement of the testis" is the only character preventing him from identifying his specimens as *D. mirabilis*. Garstang has discussed testis growth and the considerable variations in its shape and position resulting from differences in the reaction to muscle bands of its anterior termination. This applies especially in *D. denticulatum*, but also in *D. gegenbauri* and *D. irtonis*. The growth of the testis in these species, he states, is parietal, which involves penetration in the body wall between the pharyngeal epithelium and successive muscle bands: the connections of muscles to the pharyngeal epithelium constitute definite obstacles to advance. An obstinate barrier to penetration may cause the terminal portion to loop back or otherwise alter direction. Of *mirabilis*, Garstang says, the testis begins as a parietal organ while in *valdiviae* it does not. It is possible, therefore,

that Sewell's specimens demonstrate an abnormal condition of the testis, due to some check during growth, with a consequent similarity to the testis of *valdiviae*. It would seem, otherwise, that the specimens are *mirabilis*. Nevertheless, as Garstang says (p. 219), "An origin of *valdiviae* from *mirabilis* by a precocious differentiation of connective tissues impeding the advance of the gill septum and the parietal growth of the testis is still conceivable."

The New Zealand material agrees with Garstang's account of *D. valdiviae* in possessing an entire, but narrowed M.6 (Fig. 7) and in the coiling of the testis about the intestine. On the other hand, Garstang illustrates the dorsal septum extending to M.6½ and the endostyle almost from M.2 to close to M.5, whereas in the New Zealand material the septum usually extended only to M.6 (once to M.6¼) and the endostyle between M.2½ to M.4½-M.4¾ (Figs. 4, 5). Although these two features bear more similarity to *D. mirabilis*, Garstang has pointed out (pp. 204, 217) that variation in the extent of both organs does occur and consequently they may not be important to the proposition that the New Zealand material is *D. valdiviae*.

OLD NURSE STAGE: Garstang (1933) successfully differentiates between the "nurse" stages of *D. gegenbauri* and *D. mulleri* by comparison of the proportional widths of the individual muscle bands when the width of each band is expressed as a percentage of the total muscle width. He finds that in *D. gegenbauri*, M.3 and M.4 dominate (with M.3 of slightly higher percentage width than M.4), and in *D. mulleri*, M.4 and M.5 are dominant. The distinctions were valid

TABLE 3
THE RANGES AND THE RATIOS OF THE LENGTHS OF BODY AND TAIL OF
Oikopleura dioica FROM NEW ZEALAND

STATION NO.	LENGTHS (MM.)				RATIOS, BODY TO TAIL LENGTH		
	Body		Tail		Maximum	Minimum	Average
	Maximum	Minimum	Maximum	Minimum			
12	1.1	0.5	3.8	3.4	3.75	7.0	5.4
32	0.9	0.7	3.9	3.1	4.3	4.4	4.35
40	1.4	1.0	5.1	3.6	3.7	3.6	3.65
Averages					3.9	5.0	4.5

TABLE 4
 WIDTHS OF M2 TO M8 EXPRESSED AS PERCENTAGE OF TOTAL MUSCLE WIDTH IN
 "OLD NURSES" FROM NEW ZEALAND

LENGTH OF SPECIMEN	TOTAL MUSCLE	WIDTH OF MUSCLES AS PERCENTAGES OF TOTAL MUSCLE						
		M2	M3	M4	M5	M6	M7	M8
mm.	mm.							
9.8	7.3	12.3	19.2	17.8	15.1	13.7	12.3	9.6
10.0	9.9	12.7	17.9	18.9	15.2	13.8	11.4	10.1
10.5	7.7	14.3	18.2	16.9	15.6	15.6	11.6	7.8
10.6	6.9	14.5	17.4	17.4	15.8	14.5	13.1	7.3
11.0	8.1	12.3	19.9	18.6	16.1	13.3	12.3	7.5
12.0	9.7	14.5	20.6	18.5	13.4	12.4	11.4	9.2
13.5	11.5	16.5	17.3	17.4	15.7	13.9	10.5	8.7
13.8	12.1	14.8	19.0	16.5	15.7	13.2	12.5	8.3
15.4	13.6	13.8	21.3	16.8	14.6	13.8	12.4	7.3
17.5	12.0	15.8	17.5	17.5	15.9	12.5	12.5	8.3
21.0	17.7	13.0	19.3	17.7	16.5	15.3	11.9	6.3
22.0	16.4	13.4	18.3	18.3	14.0	14.0	12.2	9.8
23.0	17.4	13.8	17.2	17.1	16.7	14.4	14.4	6.4
28.0	18.6	14.7	16.7	17.6	16.4	14.6	13.4	6.6
29.0	15.75	14.5	18.4	18.5	14.5	13.5	12.9	7.7
33.5	24.05	12.6	19.6	17.1	15.9	14.7	12.6	7.5
Averages		14.0	18.6	17.7	15.4	14.0	12.3	8.0

for specimens from all areas sampled, including New Zealand.

Old nurse stages (Fig. 8) occurred in the present material along with the gonozooids and phorozooids of *Dol. valdiviae*. Application of Garstang's method to specimens indicates there is affinity to the "gegenbauri type." Consistent differences from his material were evident, however, in the percentage widths of M.2, and M.6 to M.8, relative to the widths of M.3 and M.4, see Tables 4 and 5. Table 4 presents data from Lachlan material, and Table 5, from Garstang, for *D. gegenbauri*. As M.1 and M.9 were difficult to measure accurately because of variability

in the state of contraction, and also were frequently damaged, they are omitted. The omission is scarcely significant, amounting in all to some 2-3 per cent (Garstang, p. 234), and does not account for the differences between the two groups of specimens.

In Lachlan material, M.2 averages 3.7 higher than in *D. gegenbauri*, M.3 and M.4 are respectively 1.0 and 0.7 lower, M.5 about the same, M.6 somewhat lower, but M.7 shows an increase of 1.2 and M.8 an increase of 2.4. Thus the New Zealand specimens are distinguishable by the greater proportional widths of M.2, M.7 and M.8 relative to M.3 and M.4.

TABLE 5
 WIDTHS OF INDIVIDUAL MUSCLES AS A PERCENTAGE OF TOTAL MUSCLE WIDTH, FOR
 "OLD NURSES" OF *D. gegenbauri* (FROM GARSTANG)

LENGTH	MUSCLE	WIDTH OF MUSCLES AS PERCENTAGES OF TOTAL MUSCLES								
		M1	M2	M3	M4	M5	M6	M7	M8	M9
mm.	mm.									
3- 9	—	4.0	9.6	18.1	17.8	15.2	14.2	11.2	6.3	3.4
2- 6	—	1.8	9.9	18.3	18.3	16.2	14.9	12.0	6.2	2.4
6-18	—	2.7	10.6	20.3	18.6	15.1	14.1	10.7	5.2	2.8
6- 7	5.1	2.6	10.5	19.7	18.3	15.1	13.8	11.4	5.6	3.0
9-15	10.3	2.8	10.8	20.6	18.5	15.1	14.1	10.4	5.2	2.7
17-18	14.7	2.5	10.7	20.5	18.9	15.1	14.2	10.7	4.7	2.6
Averages		2.7	10.3	19.6	18.4	15.3	14.2	11.1	5.6	2.8

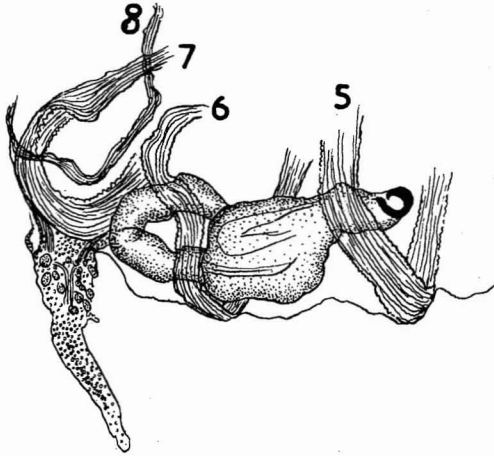


FIG. 7. *Dolioletta valdiviae*, stomach, intestine and ventral process of phorozyoid.

For the specific distinctions to be maintained, reliance is being placed on differences of proportional widths of muscle bands. It is probable that the amphiclinous condition with the myoplane (Garstang's terminology) between M.3 and M.4 would persist among other species of a particular subgenus (in this instance *Dolioletta*); and, within the condition imposed by this, it is probable also that species may be distinguishable by differences in the proportional widths of muscle bands, much as different relative widths of muscles, combined with a change in position of the myoplane, occurs between *Dolioletta* and *Doliolina*.

The occurrence together of "old nurses," gonozoids, and phorozyoids does not necessarily constitute evidence of identity. However, the "old nurses" from New Zealand consistently differ from those of a second species in the subgenus, and it is reasonable to suppose in the absence of other Doliolids, that the nurses, gonozoids, and phorozyoids belong together. It is proposed that they be considered as those of *Dolioletta valdiviae*.

Garstang has been concerned that specimens from the area of the Benguela Current which he called *D. valdiviae* might be traceable to "Some 'abnormality' of growth conditions . . ." and that "the whole of the *valdiviae* stock may have been the produce of a single swarm of nurses reared

under peculiar conditions of temperature and food supply." With the finding of specimens from New Zealand similar to those Garstang discusses, this possibility is reduced. That closely similar conditions of temperature and food supply prevailed in the two regions, and that reactions to these of the produce of some old nurses were the same, while not impossible, is unlikely.

Order DESMOMYARIA

Family SALPIDAE

Genus IASIS (Lahille)

Iasis zonaria (Pallas)

Salpa nitida Herdman, 1888

Salpa zonaria cordiformis Ritter, 1905

Salpa zonaria Metcalf, 1918; Thompson, 1948; Sewell, 1953

Fourteen specimens were collected from five stations, between Cook Strait (January) and Station 826, in the subantarctic.

Metcalf (1918) and Thompson (1948) describe and discuss this species at length. Figures 9 and 10 indicate the chief diagnostic features of the solitary and aggregate forms. As well, in solitary forms, the test is rigid, the muscles are broad and interrupted ventrally, and the body is symmetrical. In aggregate forms, the test is rigid, the muscles are widely interrupted ventrally, and the body is asymmetrical. Often one or more embryos are contained within the body.

The largest specimen was 63 mm. long, the smallest, 29 mm.

Genus THALIA Blumenbach

Thalia democratica Forskal

Thalia democratica mucronata Herdman, 1888

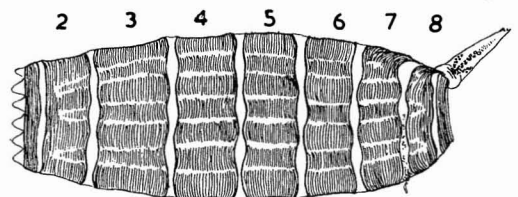
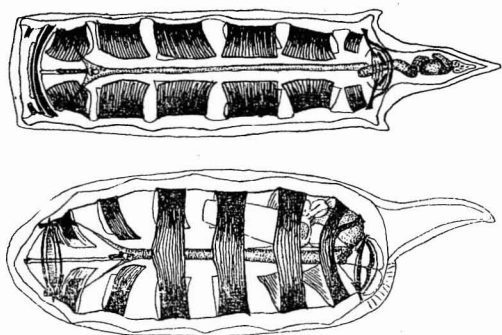


FIG. 8. The proposed "old nurse" of *Dolioletta valdiviae*, a 29 mm. specimen.



FIGS. 9, 10. *Lasis zonaria*, solitary and aggregate forms.

Salpa democratica mucronata Ritter, 1905; Ritter and Byxbee, 1905

Thalia democratica Metcalf, 1918; Thompson, 1948; Sewell, 1953

Initial collections of several hundred specimens were made at Stations 292, 301, and 304. Twelve days later, many thousands were collected from Stations 322 and 326, south of Cook Strait, in both surface and oblique tows.

The test is thickened, and often with protuberances. In solitary forms (Fig. 11) the muscles are continuous ventrally. Posteriorly the test protrudes in two long (up to the length of the body) and several smaller processes. In aggregate forms (Fig. 12) the test is greatly thickened, and with intruding tubular processes. The muscles are widely interrupted ventrally.

Solitary forms (including processes) ranged from 9.5 to 27.0 mm., and aggregate forms, from 4 to 16.5 mm. in length. Among the aggregate forms, an estimated 4 per cent possessed tests up to four times thicker than usual which made the body large and almost spherical.

Genus PEGEA Savigny
Pegea confoederata Forskal

Salpa quadrata Herdman, 1888

Salpa confoederata scutigera Ritter, 1905; Ritter and Byxbee, 1905

Pegea confoederata Metcalf, 1918; Dakin and Colefax, 1940; Fraser, 1947; Thompson, 1948; Sewell, 1953

One specimen, a solitary form (Fig. 13) oc-

curred in an oblique (100-0 m.) haul at Station 326.

The specimen was approximately 35 mm. long, but was somewhat damaged anteriorly. The test is fairly rigid, especially in the portion about the alimentary "nucleus." Four dorsal muscles are arranged in two pairs, forming "X's"; neither pair reaches the lateral margins of body. Ventral muscles are absent.

It is perhaps unusual that the only specimen captured should be the solitary form when it is recorded as rarer than the aggregate form (Ritter, 1905; Ritter and Byxbee, 1905; Metcalf, 1918; Thompson, 1948). Sewell, on the other hand, saw numerous solitary forms in the Gulf of Aden and indicates they were probably brought to the surface from deeper water by upwelling. The species is a warm water one (Thompson, Sewell) and occurred together with subtropical Copepoda, e.g., *Sapphirina* spp. in the New Zealand sample.

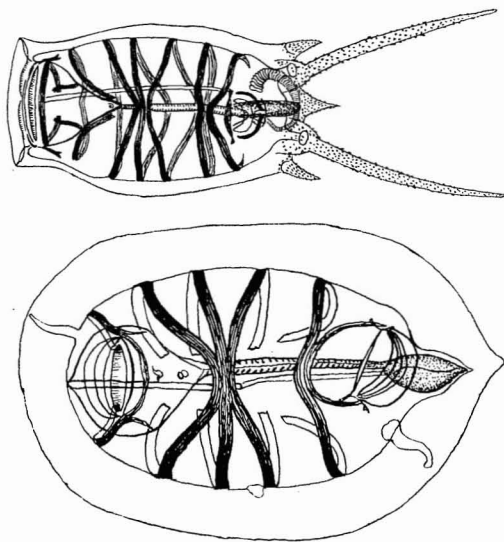
Genus SALPA Forskal

Salpa fusiformis f. *aspera* Chamisso

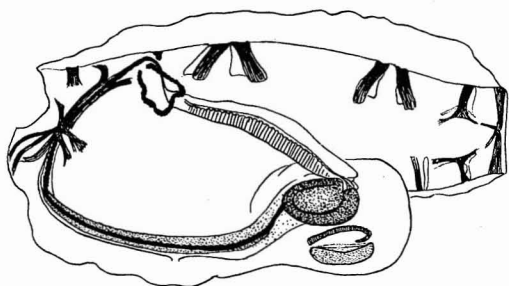
Salpa echinata Herdman, 1888

Salpa fusiformis f. *echinata* Ritter, 1905

Salpa fusiformis f. *aspera* Metcalf, 1918; Thompson, 1948



FIGS. 11, 12. *Thalia democratica*, solitary and aggregate forms.

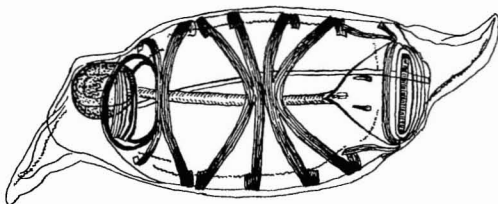
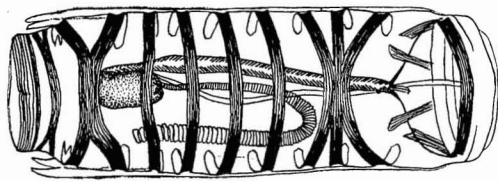
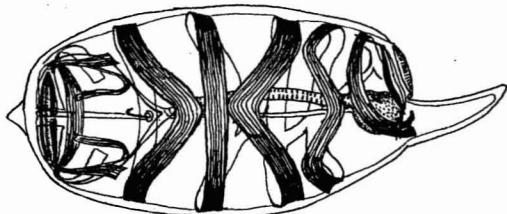
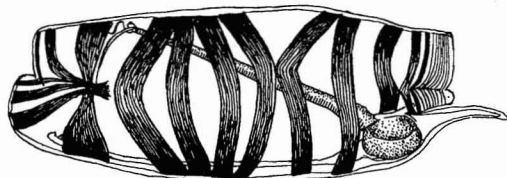
FIG. 13. Solitary form of *Pegea confederata*.

A total of 463 specimens, of which 300 occurred at Station 826, were collected from eight stations between Cook Strait (January, 1951) and the subantarctic.

Figures 14 and 15 illustrate the chief features of the species. In the solitary form (Fig. 14) the test is flaccid anteriorly, more rigid posteriorly and with several short projections. Body muscles I–III and VIII–IX are in contact dorsally, the remainder are parallel. In the aggregate form (Fig. 15) the test is more or less rigid, with elongate anterior and posterior processes. Body muscles I–IV are in contact dorsally, and IV–V laterally.

The *f. aspera* is distinguished from *fusiformis s. str.* by the ridged and spinose character of the test and processes, although on some specimens it is inconspicuous, and they could readily be mistaken for smooth forms.

Only specimens of *f. aspera* were collected by the "Lachlan."

FIGS. 14, 15. *Salpa fusiformis f. aspera*, solitary and aggregate forms.FIGS. 16, 17. *Iblea magalhanica*, solitary and aggregate forms.

Genus IHLEA Metcalf

Iblea magalhanica Apstein

Iblea magalhanica Thompson, 1948

Specimens were common in the shallow waters of Foveaux Strait and northward to Dunedin; a few occurred at Station 326, south of Cook Strait.

The test is flaccid in both forms. The solitary form (Fig. 16) has a stout, conical process posteriorly on the test. There are seven body muscles. M.I–M.IV touch, but do not fuse, dorsally and ventrally; M.IV and V touch laterally and V and VI dorsally. The test of the aggregate form (Fig. 17) has a short anterior and longer posterior process, and the body is decidedly asymmetrical. There are five body muscles. M.I–III touch dorsally and M.III and IV almost touch dorsolaterally; M.II and III, III and IV, IV and V are connected medioventrally by anastomoses; M.V is incomplete ventrally.

DISTRIBUTION AND ECOLOGY OF SPECIES

Oikopleura fusiformis

Oikopleura fusiformis is usually described as inhabiting warm, oceanic waters, although according to Thompson (1948), Lohmann obtained it in Plankton-Expedition samples from waters of 3 to 37.4 ‰ salinity, and temperatures of 9.3° to 29.5°C. The salinity range of Lachlan material (Fig. 22) is 34.15 to 34.63 ‰. The lowest temperature at which

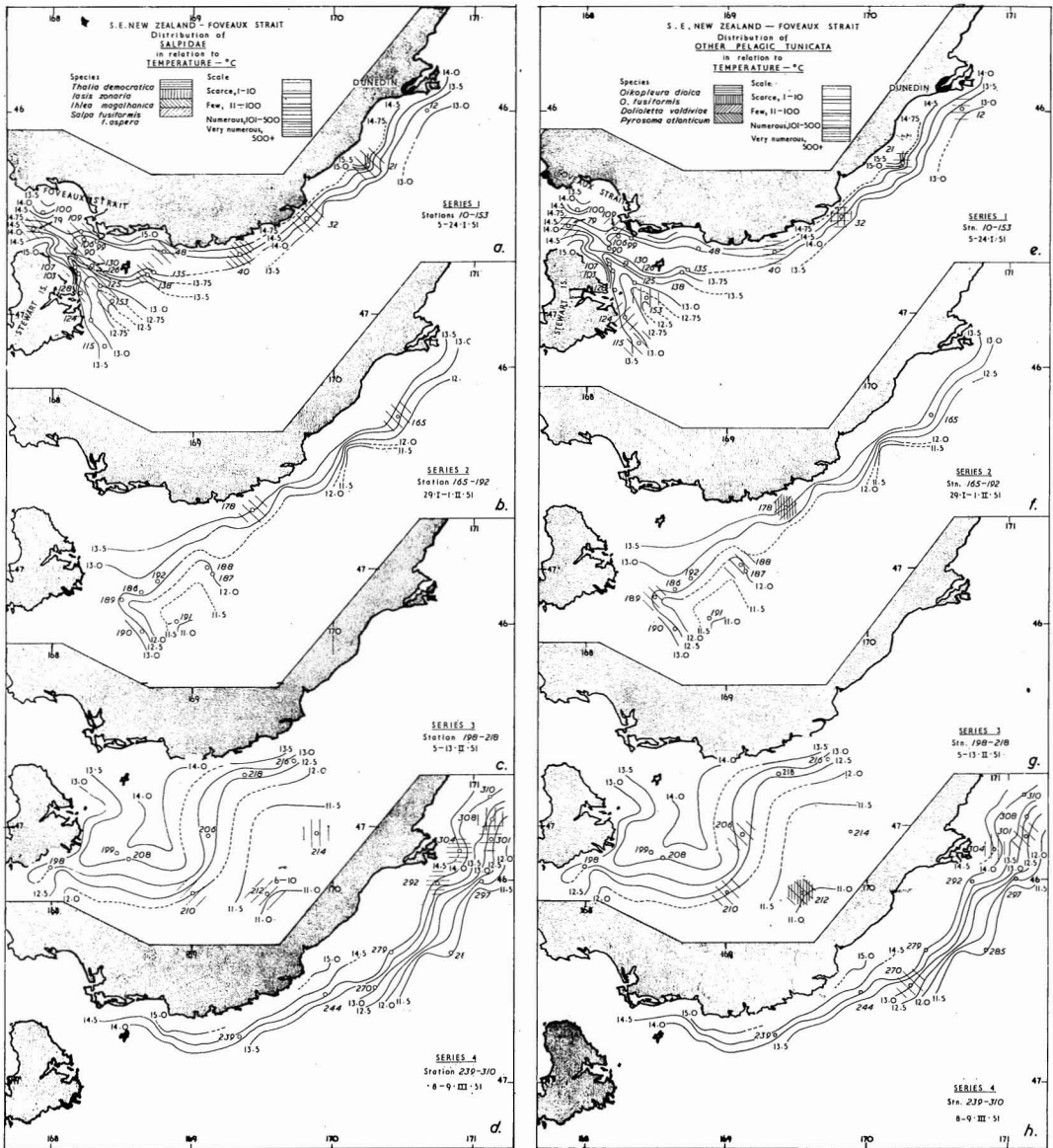
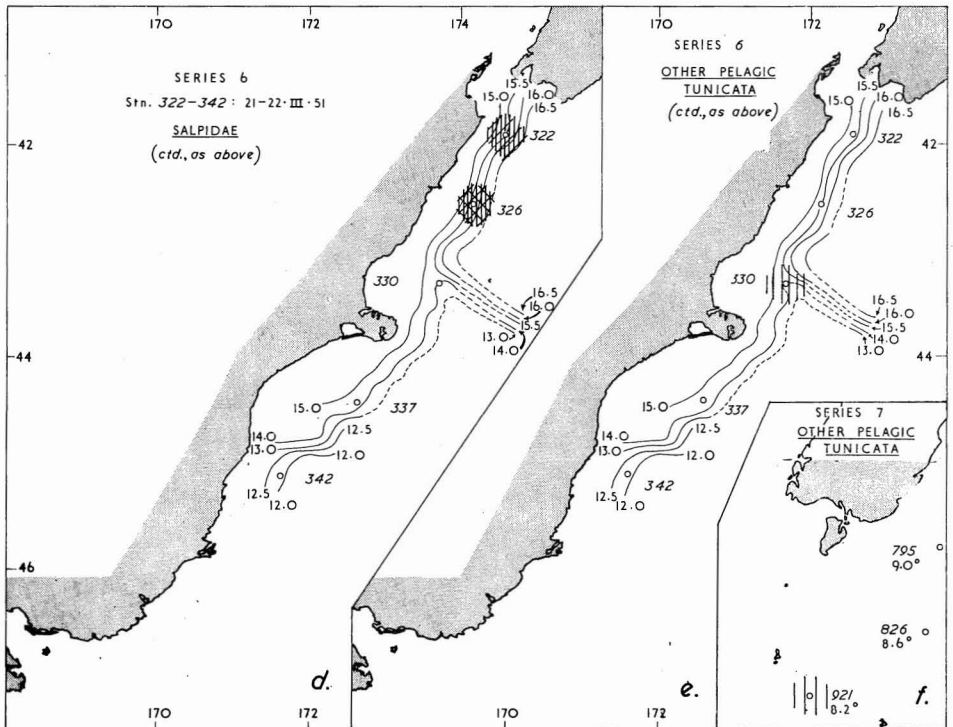
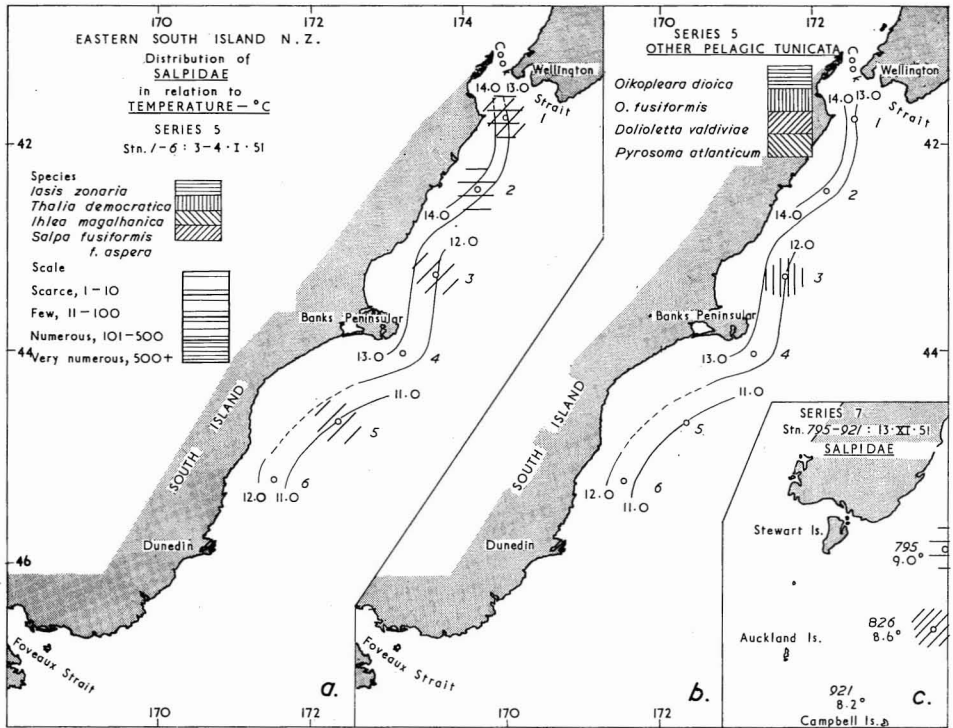


FIG. 18. Occurrences and distribution of pelagic tunicates, in relation to temperature, about southeastern New Zealand. a-c, Salpidae; e-f, other tunicates.

specimens were collected was 8.2°C. at Station 921, which is 1.1°C. lower than given by Thompson. As all the specimens were disintegrating (Essenberg, 1926b) it is possible that they had been carried into water below the lower limits of the temperature tolerance of the species.

The infrequent and sporadic occurrences of the species preclude a completed picture of local distribution. The charts in Figures 18 and 19 suggest it is being transported into coastal areas in intruding oceanic waters of subantarctic origin. Tokioka (1940) regards it as "this pure oceanic form," and the plot of its occurrence



against temperature and salinity (Fig. 22) bears this out. Over-all occurrences conform to the area of chief concentration being coincident with that of the "Southern" Subantarctic species (Fig. 20), but on the other hand, highest numbers were present in the area of the "Northern" Subantarctic species. The narrow limits of salinity (34.15 to 34.63 ‰) in which it is present are within those of subantarctic water (Deacon 1937). The temperature range of 8.2° to 14.5° C. is indicative of some degree of tolerance, but it would appear that specimens are being carried into the warmer coastal waters (e.g., Stations 330, 304) in water of subantarctic origin. The very numerous specimens at Station 178 are in coastal water, but evidence from occurrences of other species suggests that mixing may have taken place in this vicinity at an earlier time. Specimens possibly are resident in the subantarctic water (compare *Thysanoessa gregaria*; Bary, 1959a) which would extend the usual "warm-water" habitat to include a "cool-water" habitat about southern New Zealand. On the other hand, the species may have been carried southward from warmer northern waters, e.g., from the Tasman Sea. The disintegrating specimens from Station 921 lend support to such a suggestion.

Oikopleura dioica

O. dioica usually inhabits mixed, tropical and warm waters, but prefers coastal areas to the open ocean (Essenberg, 1926a: 486; Thompson, 1948: 39). The few occurrences in Lachlan samples also indicate adherence to coastal waters (Fig. 18e, and see Bary, 1959a). Temperatures are usually higher than for *O. fusiformis* (Fig. 22). It is believed that when *O. dioica* was collected with *O. fusiformis* (Stations 79, 330) (or when it occurred in water of similar properties to that from which *O. fusiformis* was captured) it was the result of coastal water having become mixed with water of subantarctic origin.

For neither *O. dioica* nor *O. fusiformis* from New Zealand is there enough information to show whether there is variation of numbers during January, February, and March, nor whether

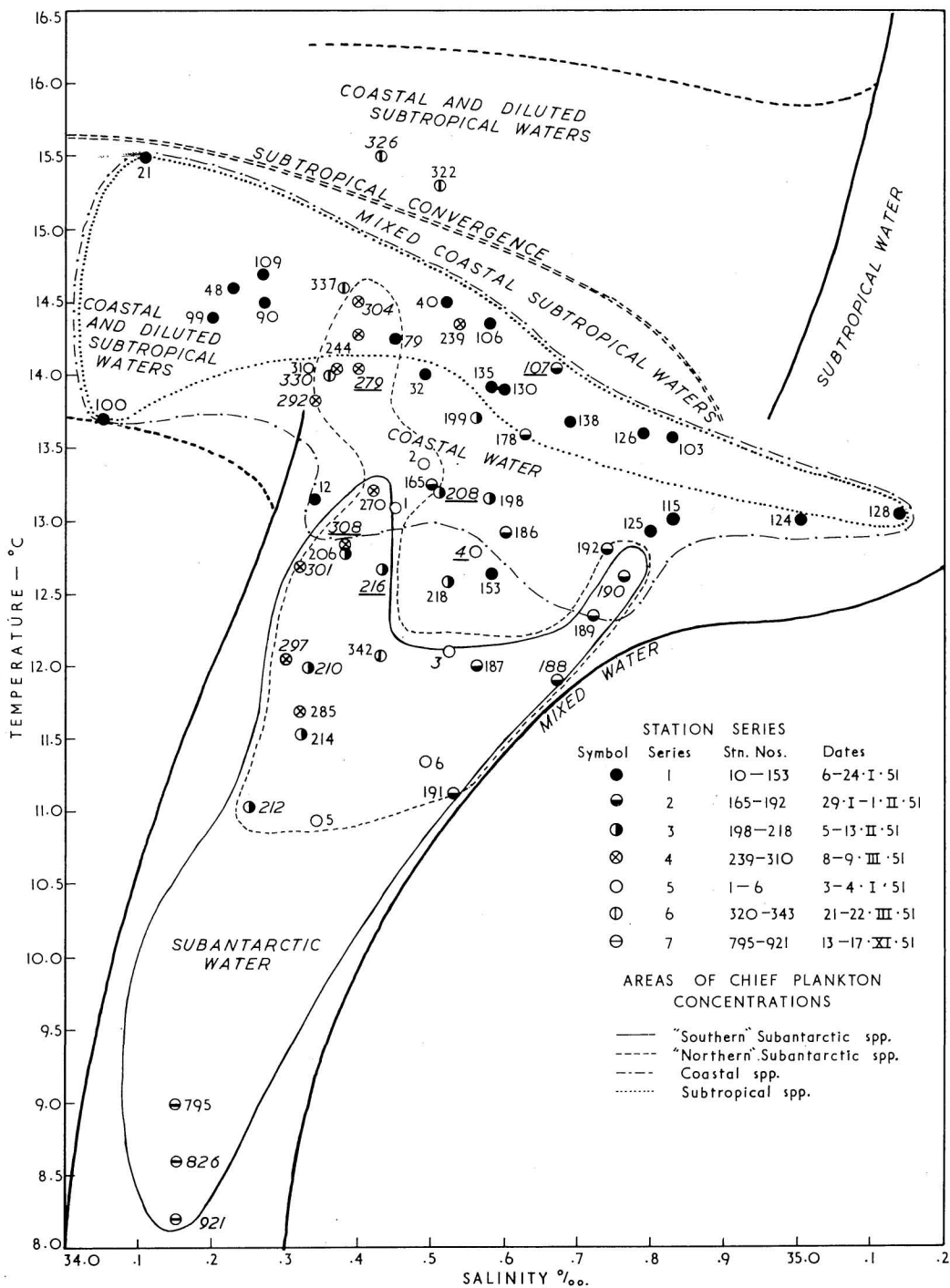
their distributions are related to the depth of water as one proceeds offshore (Bary, 1959b).

Pyrosoma spp.

Very extensive shoals of *Pyrosoma*, almost entirely *P. atlanticum*, were encountered between 10 and 20 miles seawards from Dunedin in late March and during April, 1951. Almost all specimens were aggregated into long lanes, or smaller or larger patches (Bary, 1953). Patches and lanes might occur over an extensive area at the surface, but when proceeding through a particular concentration, the colonies were seen to become progressively deeper in the water, eventually passing from sight. Oblique tows consistently collected large numbers, however, which suggests that the concentrations of specimens continued at depth. Such a vertical and horizontal distribution bears a striking resemblance to the hypothetical distribution of swarms of salps proposed by Hardy (1936: 519, fig. 7), and is of interest in relation to Sewell's (1953: 85) comment that *P. atlanticum* is "most common at some depth below the surface." The concentrations continued over several days, sometimes a number being present, at others, only one or two. Similar large shoals have been reported on several occasions from about Cook Strait. It is possible therefore they are a regular summer feature, at least along the eastern South Island coast.

The stomach contents of two fish, Blue Cod and Hapuku (*Parapercis colias* and *Polyprion oxygeneios*), caught by hand line off Stewart Island in February, confirmed fishermen's reports that *Pyrosoma* (the so-called "jelly" or "oatmeal") was common in late summer and autumn, to the extent that their catches were often depleted through the fish "being overfed and not biting." Of several hundred cod stomachs examined all but a few contained *Pyrosoma*, to about 8 cm. long. The colonies therefore must be counted as an important, although only seasonally abundant, fish food in this area. Off Dunedin, very large shoals of fish were present at the surface among the *Pyrosoma* aggregations, but it could not be verified that *Pyrosoma* was in fact being taken as food.

FIG. 19. Occurrences and distribution of pelagic tunicates in relation to temperature, between Wellington and the Auckland-Campbell Islands, New Zealand.



Charts of the occurrences of *P. atlanticum* (Fig. 18*f-b*) indicate that it may be entering coastal areas in water of subantarctic origin, but when plotted against salinity and temperature (Fig. 22) the collections are seen to occur indiscriminately in coastal and "Northern" Subantarctic waters. Specimens were also collected from stations near Station 826 (not recorded herein) in the subantarctic. Such occurrences agree with Sewell (1953: 85) who says that *P. atlanticum* is common throughout the oceans between temperatures of 7° and 30° C.

Doliolum (Dolioletta) valdiviae

Dolioletta valdiviae was present in that part of Foveaux Strait (Fig. 18*e, f*) in which coastal water is believed to be most directly influenced by water of subtropical origin (Bary, 1959*a*). Its few occurrences when plotted against salinity and temperature (Fig. 22) are in the warmest water, which together with its absence from samples elsewhere about southern New Zealand, suggest a warm-water origin for the species. More data on occurrences of the species about New Zealand and information on its distribution elsewhere are needed.

Iasis zonaria

This is a widely distributed species which Sewell (1953) regards as being carried from tropical to colder waters by currents. However, Thompson (1948) believes the species is more usually found in the deeper, colder waters in tropical or subtropical regions. It was plentiful off southeastern Australia (Thompson), but was commonest from the temperate waters of the Tasmanian area. In each year from 1939 to 1941 it decreased towards the north and this was interpreted as resulting from the increasing effects of subtropical conditions northwards. Russell and Colman (1935) recorded one specimen of the solitary form from 200 m. outside the Barrier Reef; Dakin and Colefax (1940) recorded specimens for September only, which is in agreement with Thompson's statement that

the period of greatest abundance is in the spring (August or September to November or December).

Iasis zonaria is scarce in Lachlan samples (Fig. 18*d*). Occurrences, when plotted against salinity and temperature (Fig. 21) indicate a restricted range of salinity (ca. 34 ‰ to 34.5 ‰) and a preference for lower temperatures, features suggesting the species was collected from water of subantarctic origin. This would lend support to Thompson's belief that the species is a temperate-water one. The New Zealand records are too few to be more than suggestive.

Thalia democratica

Metcalf (1918) distinguishes between western Pacific and Atlantic forms of aggregate specimens of *Thalia democratica*. The Pacific form possesses a variable number of tubular test processes, and the test is rounded posteriorly to the alimentary "nucleus." The Atlantic form possesses few, and shorter, tubular processes and the test is pointed posteriorly. Sewell (1953) points out, however, that the test varies considerably among his specimens from the Indian Ocean. The Lachlan specimens had from zero to several tubular processes, most of which were short; none possessed a posterior process approaching the length illustrated by Metcalf for specimens from the Philippine Islands. This, and the pointed test posterior to the "nucleus" suggest they may have been of the "Atlantic" form. Thompson (1948) reported that the "West Pacific" form predominated in a collection from Kaipara Harbour, northwestern North Island, and it has since been collected in Hauraki Gulf on the east coast of North Island (unpublished data). Northern New Zealand is predominantly influenced by subtropical waters (and on the east coast, possibly even by water of tropical origin) and probably this form has been transported into these areas in these waters. In the south, the water is cooler and preponderantly of subantarctic origin. The distinctions in the shapes of the tests between north (Thompson's

FIG. 20. Generalised Temperature-Salinity-Plankton diagram of the sampled area. Only the plankton stations are shown; they are differentiated into series of stations which in turn are shown individually in Figures 18, 19. "Areas of chief concentration" (as demonstrated by all of the indicator species utilised) are also shown. Station numbers *in italics* are night stations; in *italics and underlined*, are dawn or dusk stations; unmarked are daylight stations.

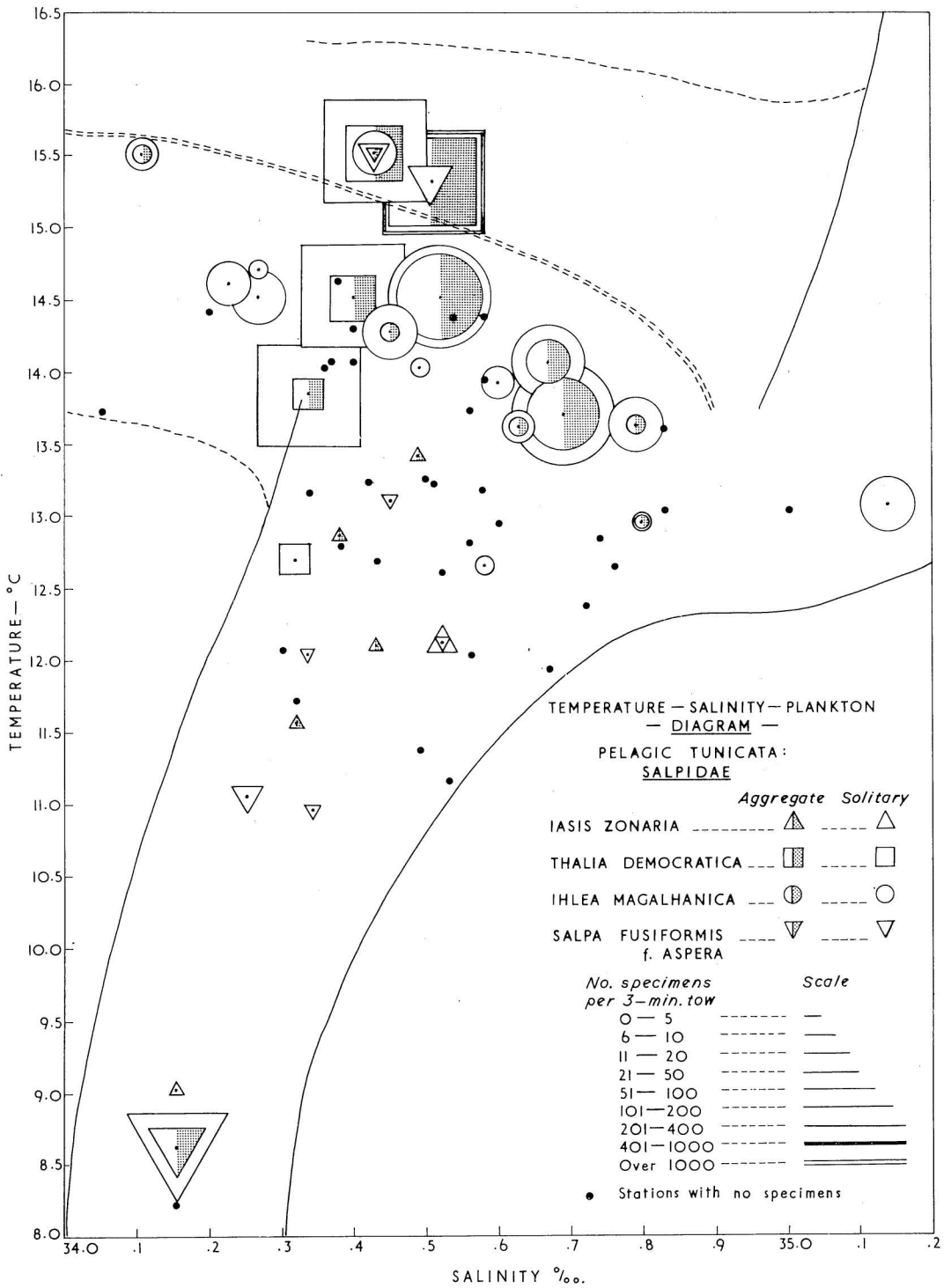


FIG. 21. Temperature-Salinity-Plankton diagram showing occurrences of species of Salpidae.

specimens) and south (Lachlan specimens) may thus result from the different environmental conditions.

The species made a sudden appearance, in large numbers, off Dunedin in early March (Fig. 18*d*). Twelve days later several thousands of specimens were taken from near Cook Strait in waters of subtropical origin. There was a complete absence of specimens in either surface or oblique tows between the areas. Morphological distinctions of a consistent nature could not be shown between these groups. Nor was it possible to demonstrate whether the concentrations were of similar origin. The plot of occurrences against salinities and temperatures (Fig. 21) indicates that the species was collected from a narrow range of salinity and from the warmest water. Indications are that the species is a warm-water one, which would be in accord with previously known facts of its distribution. For example, Thompson (1942, 1948) states that *T. democratica* occurred between temperatures of 11.0° and 25.6°C., but in very much smaller numbers in the cooler Tasmanian waters (limit, 44° S.) than in waters further north. Although New Zealand collections were from further south than those in Australia the lowest temperature was about 12.75°C. which is above the lower limit given by Thompson.

Salpa fusiformis f. *aspera*

Metcalf (1918) records *S. fusiformis* f. *aspera* as widespread in Atlantic, Pacific, and Indian oceans, from equatorial waters to those of high latitudes. Thompson (1948) records four specimens of f. *aspera*, but very large numbers of *S. fusiformis* from southeast Australia (he also took *S. fusiformis* from stomachs of "blue cod" (*Parapercis colias*) caught in western Cook Strait, New Zealand, in 1940). Lachlan specimens were entirely f. *aspera*, which reverses the order of catch recorded by Thompson, and is in line with Metcalf's statement that *aspera* was more abundant than the smooth form in his catches.

Specimens were collected from Cook Strait (in January) to the subantarctic (Station 826) where a considerable catch was made (Figs. 18*c*; 19*c*, *d*). The occurrences, plotted against salinity and temperature (Fig. 21), show that

specimens were captured from salinities commensurate with those of water of subantarctic origin. They occurred over a wide range of temperature, but even so, the T-S-P diagram strongly suggests a subantarctic origin. Both temperature and salinity ranges include Stations 322 and 326. Specimens at these stations, which are north of the subtropical convergence, may have reached the surface from water of subantarctic origin lying below the surface subtropical water (Bary, 1959*a*).

Iblea magalbanica

This species was present in very large numbers off southeast Australia, with highest concentration off eastern Tasmania where it replaced *T.b. democratica* (Thompson, 1948). Thompson also recorded it as the only salp from a collection made in 1942 from northern South Island, New Zealand. Previous to these records, it was regarded as rare, being known only from the Cape of Good Hope and Strait of Magellan, from near Kaiser Wilhelm Land and from off the south of South America (Metcalf, 1918; Thompson, 1948). Sewell (1926) is quoted by Thompson as saying the genus *Iblea* has probably adopted a cold-water habitat and that its surface distribution is limited, at any rate largely, to circumpolar regions.

Thompson (1948) in discussing the Australian records of *Iblea magalbanica* concludes that "it is one of the salp species which has a low tolerance of warm-water conditions" and, "this species will therefore probably be useful as an indicator of any northern extension of the colder type of water conditions which may from time to time occur." The temperatures in the region of its occurrences ranged between 11.6° and 22.25°C., the lower limit being relatively cool, for Australian conditions. He regards it as limited almost entirely to the upper 50 m. of water and states that maximum numbers occurred between October and February.

Twenty-five Lachlan samples yielded 1,192 specimens. Their distribution shows fairly conclusively that *I. magalbanica* is a warm-water rather than a cold-water species, at least about New Zealand. Its occurrences were in the warmest water (Figs. 18*a*, *b*; 19*d*); these included Station 326 outside of the immediate vicinity of

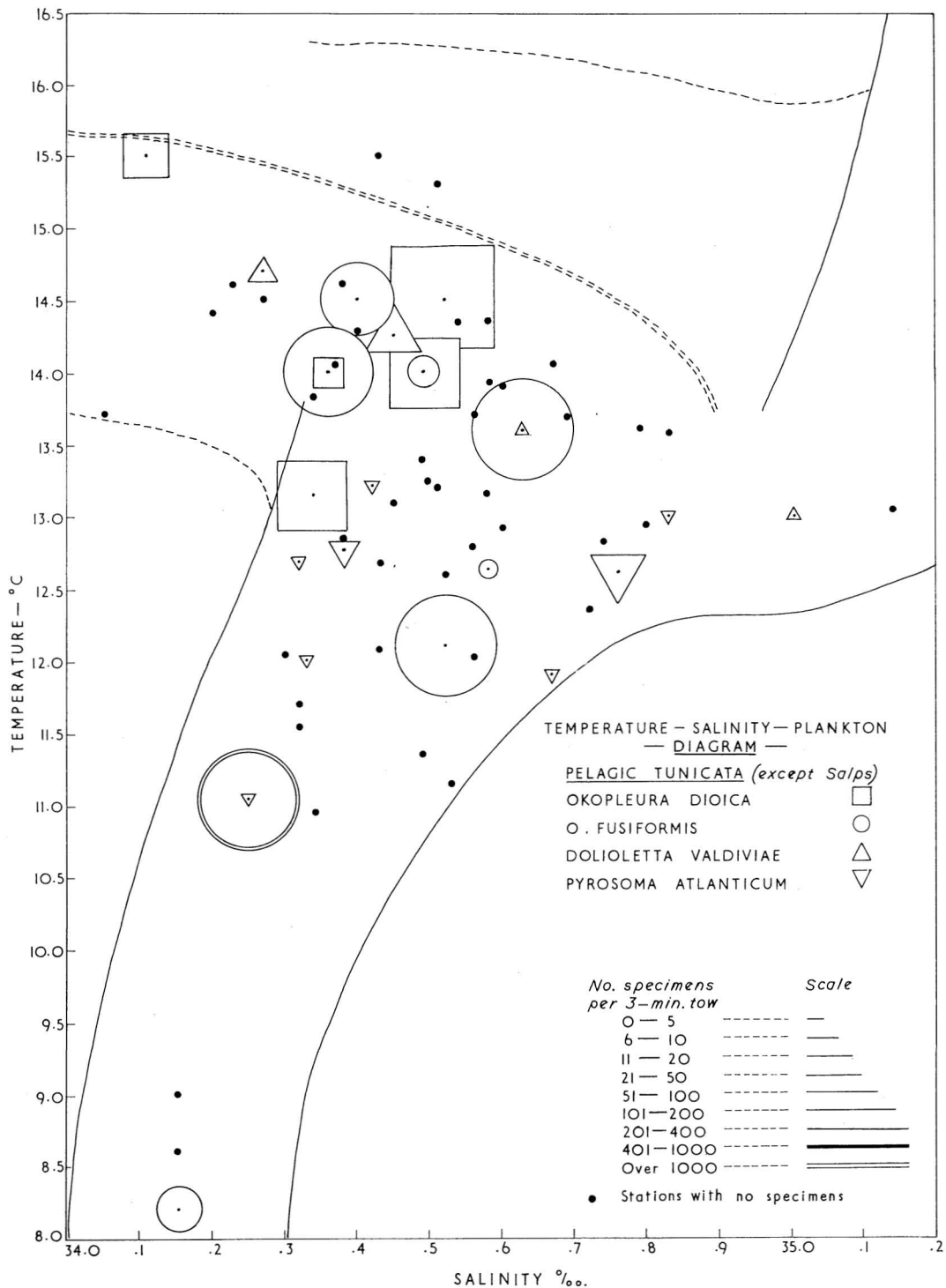


FIG. 22. Temperature-Salinity-Plankton diagram showing occurrences of species of pelagic tunicates other than salps.

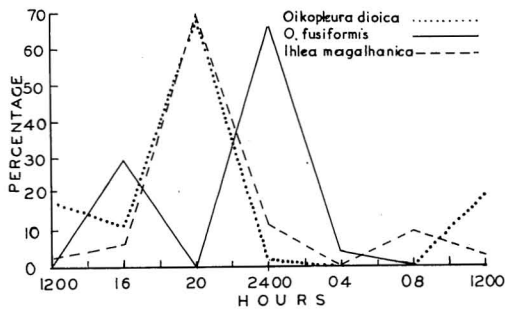


FIG. 23. Diurnal variation of numbers of specimens (collected at the surface) of *Oikopleura dioica*, *O. fusiformis*, and *Iblea magalbanica*, as shown when the average catch per four-hour period is expressed as a percentage of the totalled average catches.

Foveaux Strait in water of subtropical origin (where it occurred with *Thalia democratica*). Again, when occurrences are plotted against salinity and temperature (Fig. 21) a distinct preference is demonstrated for the warmest water, which Bary (1959a) regards as being influenced by water of subtropical origin. The temperatures given by Thompson (11.6° to 22.25° C.) are inclusive of the range for subtropical water, given by Deacon (1937). The evidence from the present material, and possibly that from Thompson also, suggests the species may have subtropical, rather than cold-water origins.

DIURNAL MIGRATION

As the collections being considered are from the surface waters, diurnal migration can only be inferred from the variation of numbers between day and night samples. *Oikopleura dioica*, *O. fusiformis*, and *Iblea magalbanica* occur spasmodically, but if the average four-hour catch is plotted as a percentage of the totalled average catches (Fig. 23) some smoothing of their occurrences is introduced. It is then found that *O. dioica* and *I. magalbanica* increase to a high percentage in the early evening (at 1800 to 1900 hours in untreated data). *Iblea magalbanica* is present otherwise in comparatively small numbers, while *O. dioica* tends to occur throughout the day. *Oikopleura fusiformis* was present in markedly high numbers at 2400 hours (2400 to 0100 hours in untreated data), and again, but in lower numbers, at 1600 hours

(two peaks, one at 1500 and the other at 1700 hours, in untreated data). Thus there are indications that numbers increase towards evening, or during darkness. However, the shoaling of salps, and, to judge from their irregular appearances, a tendency to swarming among appendicularians, makes any other than these tentative conclusions unwarranted.

In connection with vertical migration among tunicates, Russell and Colman (1935) showed that in the area of the Great Barrier Reef appendicularians migrated to near the surface between 2100 and 2325 hours and sank during daylight, when they concentrated at about 10 m. Mackintosh (1934: 94) and Hardy (1936: 521) illustrate and discuss vertical migration among salps, including the effects of swarming. It is shown that increases occur at or near the surface around midnight if due allowance is made for the existence of the swarms. It is probable, therefore, that the increases illustrated in Figure 23 to some extent are the result of vertical migration, although further sampling will almost certainly refine the patterns obtained.

Variation of numbers at the surface is shown by *Doliioletta valdiviae* for Stations 74 to 85 (at these stations the net was streamed in a tidal stream whilst the ship was at anchor, see Bary, 1956). The combined gonozooids, phorozooids, and old nurses (Fig. 24) increase in numbers to a peak at 2200 hours, decline to zero at 2400 hours, and increase to a second peak at 0200 hours. Data concerning doliolids for Station 83

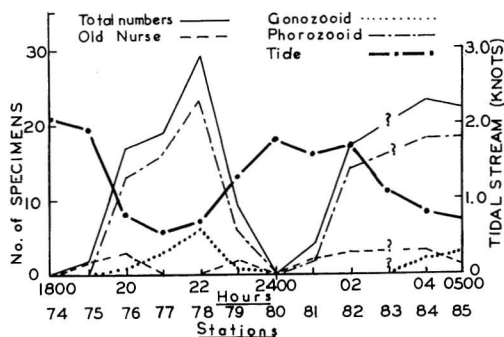


FIG. 24. Variation of numbers of the gonozooid, phorozooid, old nurse, and totalled specimens of *Doliioletta valdiviae*, during the course of one night when the ship was anchored and the net was streamed in a tidal stream.

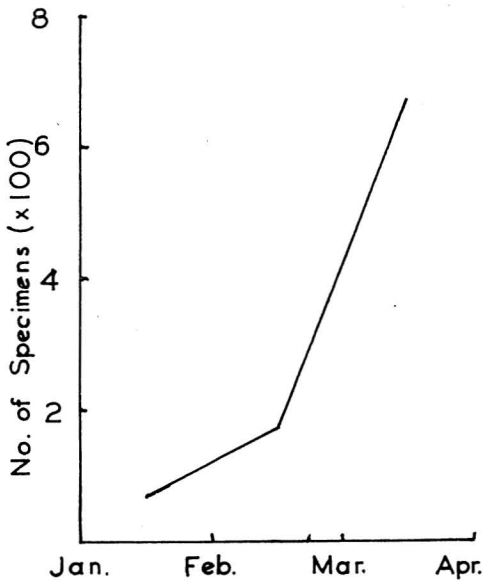


FIG. 25. Variation in average number of specimens per haul of all species of tunicate for January, February, and March, 1951.

are lost, and curves have been continued to Station 84 (0400 hours), but are queried. High numbers were still present at 0400 and 0500 hours, when sampling was discontinued. Individually, phorozoids, gonozoids, and old nurses show somewhat similar patterns to the average and to each other. More data are necessary to verify that the results illustrated are, in fact, the result of diurnal migration. Each of the peaks of numbers shows a degree of correlation with low tidal velocities which may not be coincidental, although reasons for this are not clear.

TUNICATES AS INDICATOR SPECIES

Results accruing from Lachlan samples on the use of salps as practical indicator species are meagre. Distinct preferences are apparent when occurrences are plotted against salinity and temperature (Figs. 21, 22) and some of these probably would persist, even with more samples, e.g., as for *Iblea magalbanica* and *Iasis zonaria*. Most of the species of tunicates cannot be regarded as practical indicators in that they occur so spasmodically. In conjunction with other 'Indicator Species,' as demonstrated in T-S-P diagrams, some of them provide useful additional evidence of the presence of particular

waters, e.g., *Thalia democratica* and *Iblea magalbanica*.

Distinctions between the faunas on either side of the subtropical convergence are not evident from the distribution of the tunicates.

On the other hand, distinct "coastal" and "oceanic" faunas appear to exist; the former consisting of *Iblea magalbanica* and *Oikopleura dioica*, and the latter of most of the remaining species. How such relatively passive planktons are able to maintain these distributional distinctions, especially in the strong tidal currents existing about the southern coasts of New Zealand, is a problem. Boden (1952), Hart (1953), and Bary (1959a) suggest that differential circulation between near and offshore waters may exert considerable influences.

SEASONAL DISTRIBUTION

The very spasmodic appearance of the majority of species of tunicates makes it difficult to indicate the nature of their seasonal distribution for January, February, and March, 1951. Average numbers taken per tow, of all species, do show a sharp increase to March (Fig. 25). This average condition, however, masks a number of species irregularities. For example, *Pyrosoma atlanticum* appeared late in January (one specimen), and increased in numbers steadily to March; *Salpa fusiformis* f. *aspera* occurred in early January, again at the end of February, and again at the middle and end of March; *Iblea magalbanica* occurred in January, and again in March, and so on. Some of the increases in the numbers of specimens are almost certainly seasonal, but irregularities such as result from the sampling of swarms tend to produce a misleading picture for most species. To be reliable, data would need to be available from several seasons. Similar irregularities in catches, and their effects on curves of their distribution, are illustrated for several salps from the Barrier Reef by Russell and Colman (1935).

SUMMARY

Notes are given on the systematics of *Oikopleura dioica* and *O. fusiformis*, *Doliolum* (*Doliolletta*) *valdiviae*, *Pyrosoma atlanticum* and *P. spinosum*, and of the salps *Iasis zonaria*, *Thalia democratica*, *Pegea confoederata*, *Salpa fusiformis* f. *aspera*, and *Iblea magalbanica*. The

"old nurse" stage of *Dolioletta valdiviae* is believed to have been collected and is described and discussed in relation to the "old nurse" of *D. gegenbauri*. Occurrences in relation to temperatures and salinities, and the distribution of species in New Zealand waters, are discussed.

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