Distribution and Ecologic Aspects of Central Pacific Salpidae (Tunicata)[1]

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THE PRESENT REPORT is a continuation of a general salp study, the first section of which already has been reported (Yount, 1954). It concerns the distribution and ecology of the salps collected during two cruises by the "Hugh M. Smith" of the Pacific Oceanic Fishery Investigations of the United States Fish and Wildlife Service (referred to in the remainder of this report as POFI) in the central Pacific Ocean. Nineteen out of a total of 22 recognized world species were found in these collections.

Knowledge of the distribution of salps was reviewed by Traustedt (1885), Apstein (1894, 1906), Metcalf (1918), Ihle (1935), and Thompson (1948). Various other investigators have added to this general knowledge in regard to certain species. Certain points in regard to geographic distribution, however, needed clarification. Among these was an investigation of the usefulness of salps as indicator species of oceanic currents within the area of study. Moreover, knowledge of seasonal effects on salps, of the relation of salp abundance to the abundance of other zooplankton, and of the relation of salp abundance to physicochemical environmental factors was very limited. Thus studies were carried out, insofar as the available data would permit, in an attempt to elucidate these points. In addition, little information exists defining the actual role or position of salps in the plankton community (the niche as defined by Elton, 1927); consequently, the niche of the different salp species was investigated as thoroughly as possible.

ACKNOWLEDGEMENTS

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MATERIALS AND METHODS

The animals used were taken from a large series of plankton captures made by POFI in an area that extended from 27° N. to 15° S. and from 176° W. to 155° W. In this area, the "Hugh M. Smith" made cruise 5 in June, July, and August of 1950, and cruise 8 in January, February, and March of 1951, thus permitting seasonal comparisons. The study of abundance and distribution was confined to cruises 5 and 8; of these cruises, all samples (51) from cruise 5, and 30 samples out of 106 from cruise 8, were studied.

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The total plankton data used here were reported by King and Demond (1953); Cromwell (1953, 1954) reported all hydrographic observations used here. As King and Demond stated, the plankton net descended obliquely to 200 meters, then made an oblique ascent to the surface. Thus the net strained, during approximately 30 minutes, a total of about 1,000 cubic meters of water. This net was described in King and Demond's report as being 1 meter in diameter, with a mesh width of 0.65 mm., but I should point out here that it was an open net. For this reason, vertical distribution of the captured animals is unknown.

All animals larger than about 5 cm. were removed from each POFI plankton sample (King and Demond, 1953). The sample was then divided into two equal portions, one of which was not used by POFI personnel. The latter portions were used for the present study. Therefore, in calculations where comparisons were necessary, salp numbers and volumes were estimated by doubling the figure obtained from each half sample. In addition, many of the removed salps larger than 5 cm. were examined and identified. Number determinations of salps were made by direct counting, whereas volume determinations of the salps were made for each plankton sample by means of water displacement in a graduated cylinder. In order to determine the relation between salp volume and volume of the other plankton in the same sample, the salp volume determinations were divided by the amount of water strained (taken from King and Demond) and compared with the total volumes of zooplankton, less salps, reported by King and Demond.

ABUNDANCE OF SALPS

Physicochemical Factors of the Environment

A study of the ecology of salps should consider all aspects of their environment such as food, enemies, and the distribution of physicochemical factors of the waters in which they are found. Of possible direct importance to them is the distribution of temperature, density, currents, salinity, and oxygen. On the other hand, distribution of light and of nutrient chemicals, factors which influence phytoplankton production, is probably only indirectly important to salps. Which among these are limiting factors for salps is almost wholly unknown.

In the open ocean, salinity is presumed not limiting because of its small variation, from about 34 to 36 °/oo. Salps seem to be absent from areas of very low or high salinity, such as may be found in certain waters. For example, Apstein (1906) reported no salps from the region off the mouth of the Congo River in Africa, a situation apparently related to the low salinity (30.4 °/oo) in the area; and Ihle (1935) noted that some species of salps were absent from the eastern part of the Mediterranean Sea, perhaps indicating a relationship to the high salinity (up to 40 °/oo off Syria).

In regard to temperature, also, little is known about limits of tolerance for the various species, although all salp species—except an antarctic form, *Ihlea magalhanica*—are found principally in warm regions of the ocean. Occasionally they are found in high latitudes, presumably carried there by current tongues, for example, in the Bering Sea (Metcalf, 1918), the Gulf of Maine (Bigelow, 1926), the North Sea (Fraser, 1949, 1954), and waters of southern Australia (Thompson, 1948). Salps have also been found at great depths (more than 1,000 meters) where the temperature was low (Apstein, 1906; Michael, 1918; Sewell, 1926, 1953; Leavitt, 1935, 1938). The limits of tolerance for both salinity and temperature in the various species are thus unknown and can only be inferred from reports of distribution.

Factors that influence variation in organic productivity must also be considered for a clear understanding of variation in salp abundance. Areas of maximum biological productivity are found in coastal waters, in temperate and higher latitudes, and in regions of upwelling. Productivity in these areas is based chiefly on vertical mixing of the waters (Sverdrup, *et al.*, 1942: 785; Tait, 1952: 76; Harvey, 1955: 99) and additions of dissolved nutrients from the land (Künne, 1950: 57; Dakin, 1952: 7), which bring nutrients to the euphotic zone where they can be used. In temperate waters, vertical mixing and resultant enrichment are useful for production principally in the spring and fall; in midwinter the standing crop of organisms is low, due primarily to insufficient light intensity, while in midsummer the low standing crop is apparently the result of depletion of nutrients in the euphotic zone (Russell and Yonge, 1936: 246). In tropical waters, on the other hand, there is generally a low concentration of nutrients in the euphotic zone with an attendant low standing crop throughout the year, apparently because upper tropical waters (to a depth of about 300 meters) are characterized by a three-layer system—an upper warm layer, a transition layer, and a lower cool one—present during a large portion of the year. Thus sinking of decomposing substances from the surface layer to a depth below the transition layer results in a removal of nutrients from the euphotic zone until vertical mixing of the waters again brings the nutrients back.

The enrichment in the zone between about 2° N. and 5° S. in the area studied undoubtedly originates principally from vertical water movements; i.e., it probably does not originate in the Peru Current from the east. The phosphate and standing crops of the region studied probably also reflect, in small part, a horizontal movement of water from the east. No quantitative data on the westerly limits of the effects of the Peru Current are available, but considering the great distance involved, one can assume that the phosphate from upwelling in the Peru Current is utilized long before reaching the meridians studied. In other words, the water from the Peru Current has "aged" by the time it reaches these meridians, i.e., has moved far from the upwelling which initially enriched it (Steemann-Nielsen, 1954). However, since these waters of the meridians studied are in a continuous state of upwelling they are "young," that is, they have a high concentration of nutrient chemicals, being more or less continuously replenished from below.

Another factor should be considered in regard to enrichment: phosphates probably affect salps only indirectly. As only plants are considered able to utilize dissolved nutrients such as phosphates for biological production, salps are probably affected by phosphates only by way of their food, which consists primarily of phytoplankters. Salps thus stand one trophic level away from the dissolved nutrients as shown by their trophic relationships: dissolved nutrients → phytoplankton (producers) → herbivorous zooplankton (primary consumers). Time, therefore, is required for the phosphates to be used by the phytoplankton in order that the primary consumers can be affected by the increased production. For this reason, it is possible that the salps captured at the same time would show little correlation, station to station, with the phosphates. However, the increased phosphate found in the region of upwelling is a zonal condition and thus not transient, and results in generally larger standing crops of plankton in this region (Cromwell, 1953; King and Demond, 1953).

Considering the above factors, then, one would expect increased availability of nutrients in the regions of upwelling and in other regions in which frequent vertical mixing occurs, such as in zones of shear at the edge of currents (the regions of "Ansammlungen" of Apstein, 1906), and in waters near island masses where vertical mixing and diffusion may occur as a result of eddies and where dissolved nutrients from the land may be added. Therefore, the a priori expectation for this study was that larger standing crops of salps would be related to those ecologic factors favorable to biological production.

One further subject—that of the sources of error to which the results are liable—should be discussed before a description of the meridional sections is given. King and Demond (1953) described the possible errors in regard to the total zooplankton, and a large part of the following review is based on their report.

One source of error is from the fact that estimates of each plankton sample were made by doubling the figures obtained by direct measurement and counting of the half samples. In addition to the halving of each plankton sample, another source of error comes from the removal of organisms larger than 5 cm. from each of the samples. Undoubtedly this removal of large salps has considerably reduced the volume of capture at some stations.

Day-night variation was shown by King and Demond to have had considerable influence on the total zooplankton of cruises 5 and 8, but there was no important effect of this variate on salps, at least in the 0–200 meter layer. This is in agreement with the report of Apstein (1906), who considered that, in general, salps perform no diurnal vertical migrations. One species, *Thalia democratica*, however, was considered by Michael (1918) to migrate vertically as a result of temperature variations and reproductive behavior. Hardy (1936) and Fraser (1949) have given evidence that indicates a nightly movement toward the surface, but their tows were shallower than 200 meters.

Perhaps the most important source of error is the "patchy" distribution, both horizontally and vertically, of plankters in general. Nothing is known of the extent to which the variations in capture of the plankters is reliable: i.e., there is doubt as to whether there is a true ecologic difference between the capture at one station of 1 cc. of salps/1000m^3 and the capture at another station of 1.5 or 2 cc/1000m^3. Perhaps the difference is due simply to variation that could be expected from the method of capture alone or from the patchiness of the salps. A better way to minimize this error would be to take a series of plankton tows at each station so that an average could be obtained. This was impractical for the POFI cruises. In order to minimize patchiness, on cruises 5 and 8 only oblique tows were made, as the oblique tow has been regarded by Winsor and Clarke (1940) as well as by King and Demond (1953) as more efficient than either horizontal or vertical tows. By this oblique towing method, a large volume of water was strained; King and Demond assumed, therefore, that "variation in catch due to the uneven distribution of organisms is minimized" (p. 119). However, in view of the small volumes and numbers of salps observed occasionally, the actual population density may have been quite different.

The POFI cruises traversed three principal currents in the central Pacific: the westerly flowing North Equatorial Current which arises in part from waters of the California Current; the easterly Counter Current, with its source waters primarily from the neighborhood of the southern Philippine Islands and New Guinea; and the westerly South Equatorial Current fed from the Peru Current and the Gulf of Panama. Figures 1 and 2 show this region and the stations where the plankton samples were collected. For purposes of this report, the data from cruise 5, 172° W. are used as an example of the currents disclosed by a meridional section (cf. Fig. 4). The North Equatorial Current flows mainly westerly from the Hawaiian Islands (27° N., station 1) to the northern limit of the Counter Current at about 8° N., station 14; the easterly flowing Equatorial Counter Current (from about 8° N., station 14, to 4° N., station 18); and the westerly flowing South Equatorial Current (from about 4° N., station 18) to the southern limit of the section.

Since the surface phosphate concentration is associated with the stratification of the water, which is in turn primarily dependent on the temperature, the vertical sections for these two parameters are closely related. Because the vertical temperature sections are so revealing, they are used to describe the general ecologic features to be considered with

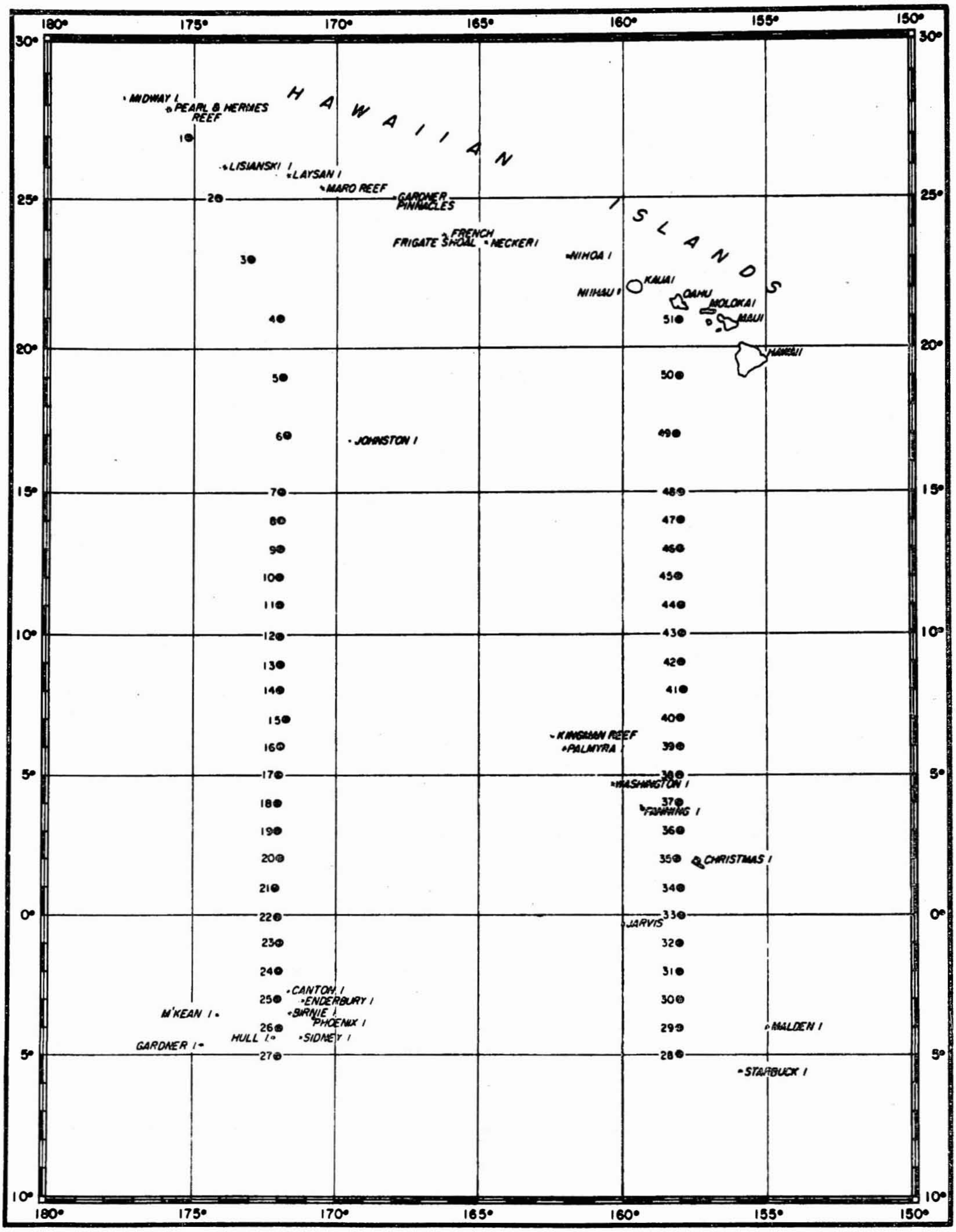
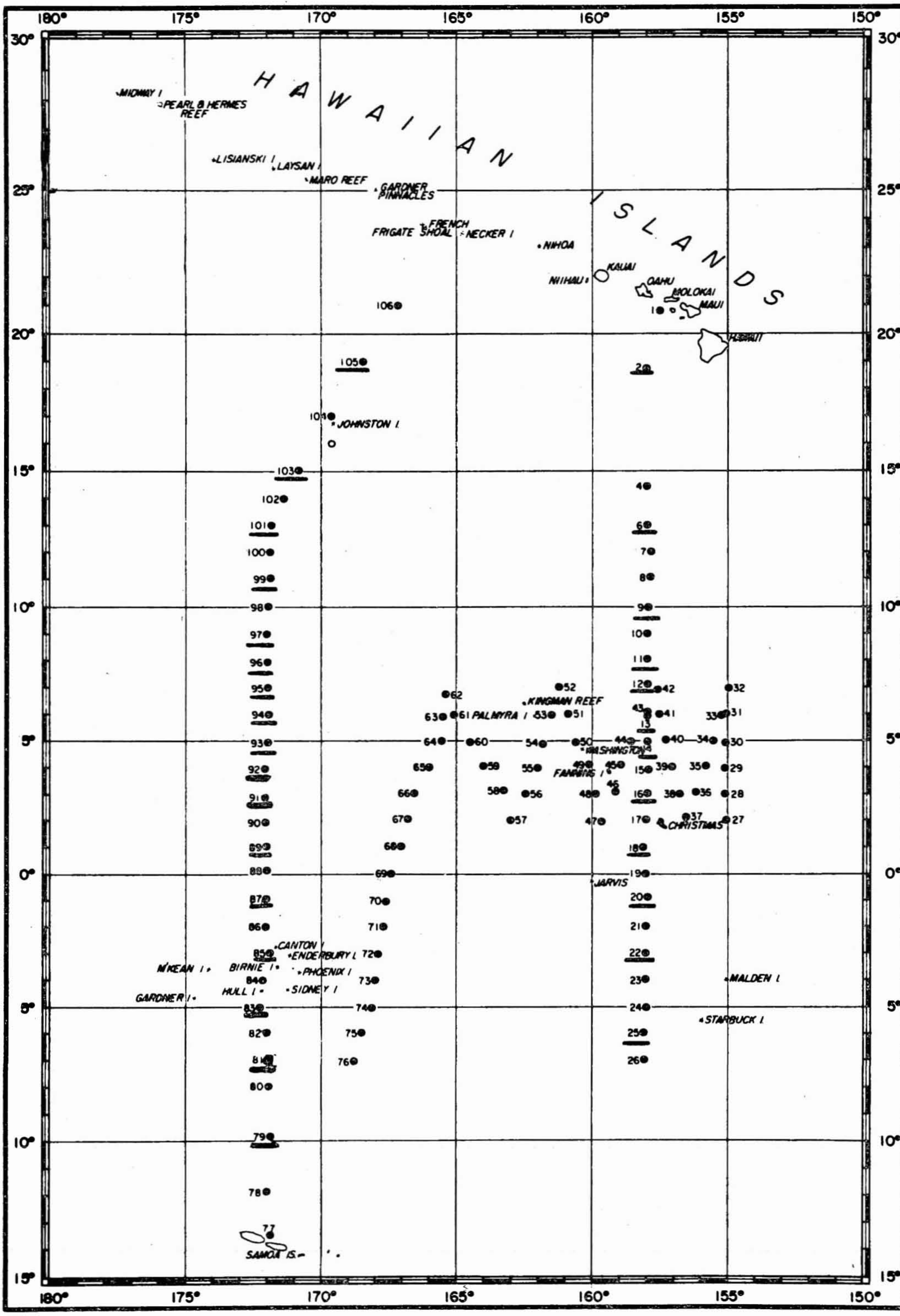


FIG. 1. "Hugh M. Smith," cruise 5; June–August, 1950. Numbers 1–51 indicate stations at which plankton tows and hydrographic observations were made. (After Cromwell, 1954.)


HAWAIIAN ISLANDS
MIDWAY I
PEARL & HERMES REEF
LISIANSKI I
LAYSAN I
MARO REEF
GARDNER PINNACLES
FRENCH FRIGATE SHOAL
NECKER I
NIHOA
KAUAI
NIIHAU
OAHU
MOLOKAI
MAUI
HAWAII
JOHNSTON I
KINGMAN REEF
PALMYRA I
WASHINGTON I
FANNING I
CHRISTMAS
JARVIS
CANTON I
ENDERBURY I
PHOENIX I
SIDNEY I
M'KEAN I
BIRNIE I
HULL I
GARDNER I
MALDEN I
STARBUCK I
SAMOA IS.
180°
175°
170°
165°
160°
155°
150°
30°
25°
20°
15°
10°
5°
0°

each of the meridional series of salp samples. It should be pointed out, however, that the distribution of the other determined factors—density, salinity, inorganic phosphates, and dissolved oxygen—is very similar on all meridians studied here (see Cromwell, 1954). The detailed descriptions of all parameters studied may be found in Cromwell (1953, 1954).

Considering the emphasis to be placed on temperature, it is desirable to describe its major variations. It was found (Cromwell, 1954) that temperature distribution in the North Equatorial Current was characterized by a relatively poorly developed thermocline. The region of the Counter Current (about 8° N. to 4° N.) was characterized by a gradual north-south sharpening of the thermocline and a deepening of this layer to the south. The northern part of the South Equatorial Current was characterized by a well-developed, deep thermocline in the region of upwelling. South of this region, the thermocline again became less well defined. Inspection of the temperature distribution (Cromwell, 1954, fig. 6) shows conical isotherms resulting from an upward transport of the cooler waters of the lower surface layer and upper thermocline from 1° N. to 2° S. This is associated with the wind-induced divergence and the attendant upwelling, as evidenced by the cooler temperature found at the surface.

As the histograms in Figures 3 to 6 show, the salps discussed herein were taken on two meridional sections during cruises 5 and 8 of the "Hugh M. Smith." The histograms show the observed variation of the total salp volume, total salp numbers, and the numbers of the commonest species, *Thalia democratica*, *Salpa fusiformis*, *Ritteriella amboinensis*, and *Cyclosalpa pinnata*. A typical section, cruise 5, 158° W., is discussed in detail and the remaining sections are compared with it.

The typical section (Fig. 3) shows that the majority of the relatively large volumes were taken from 1° S. to 4° N., in or near the region of upwelling which was characterized by low temperature and a high phosphate value. Large volumes were also taken from 17° to 21° N., apparently due to the influence of the Hawaiian Islands.

Total numbers of salps (Fig. 3*a*) showed a very different distribution from that of total volume, as can be expected, since a few large specimens may greatly influence volume but not numbers. Inasmuch as *Thalia democratica* comprised the principal portion of the total numbers at most stations, it is discussed simultaneously with total numbers. The greatest numbers were taken in the region under influence of the upwelled waters but large numbers were also taken in waters far from this region (15°N.), a fact which may be explained by the presence of a current shear and/or eddies associated with the Hawaiian Islands. The large numbers taken at 4°, 5°, and 9° N. appear to be associated with the shearing effect at the southern and northern boundaries of the Counter Current. The majority of the small numbers occurred away from the upwelled region, in regions where the previously described layered system was well developed and the phosphates in the euphotic zone were low.

The other common species show a rather different distribution (Fig. 3*b*). *Salpa fusiformis* was most abundant near the region of upwelling. No substantial influence was shown by proximity to islands. *Ritteriella amboinensis* was taken in greatest numbers near the upwelling and in regions possibly influenced by proximity to islands. *Cyclosalpa pinnata* occurred only in small numbers; nevertheless, its principal occurrence was in the region of upwelling in the South Equatorial Current. It does not appear to have been influenced by other factors examined.

The section of cruise 5, 172° W. (Fig. 4), is characterized by a more general meridional

FIG. 2. "Hugh M. Smith," cruise 8; January–March, 1951. Numbers 1–106 indicate stations at which plankton tows and hydrographic observations were made. The underlined numbers represent stations examined for the present study. (After Cromwell, 1954.)

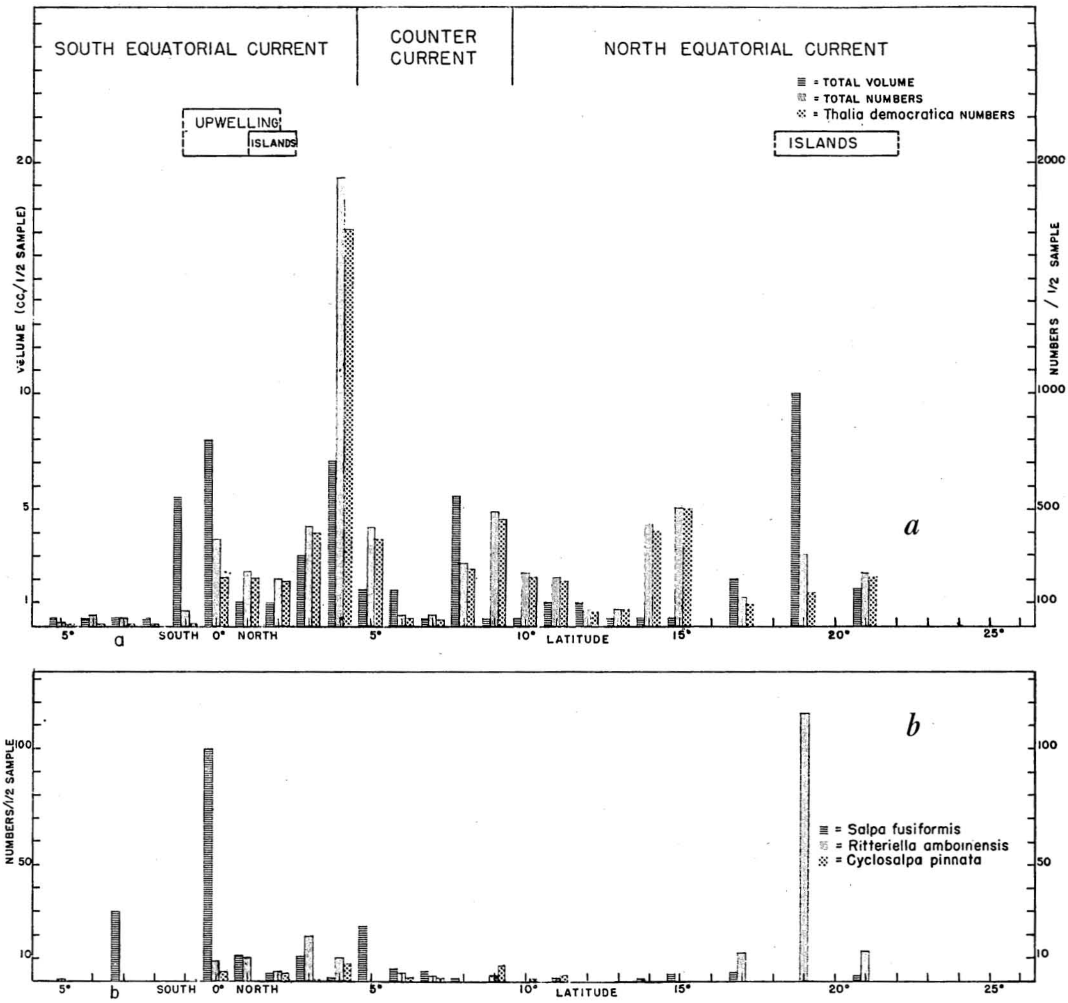


FIG. 3. Cruise 5, 158° longitude. *a*, Relationship of total salp volume, total salp numbers, and numbers of *Thalia democratica* to major currents, upwelling, and island masses. Limits of currents, upwelling, and islands are approximate. *b*, Relationship of the other common species, *Salpa fusiformis*, *Ritteriella amboinensis*, and *Cyclosalpa pinnata* to major factors listed in *a*.

distribution with indications of increased volumes near the equator, near the current shear at the margin of the Counter and North Equatorial Currents, and in waters near the Hawaiian Islands. Relatively great total numbers and numbers of *Thalia democratica* were taken near the region of upwelling and in waters near the Hawaiian Islands. The abundance of the other species shows little apparent relation to the ecologic factors being considered, but there was a tendency to greater numbers in the region of upwelling.

In regard to the section of cruise 8, 158° W. (Fig. 5), the distribution of the volumes appears to be random, showing little apparent relation to the ecologic factors examined except in one instance (10° N.), where a relatively large volume was taken in the region of current shear between the margins of the Counter and North Equatorial Currents. The distribution of total numbers and of numbers of the common species also showed little

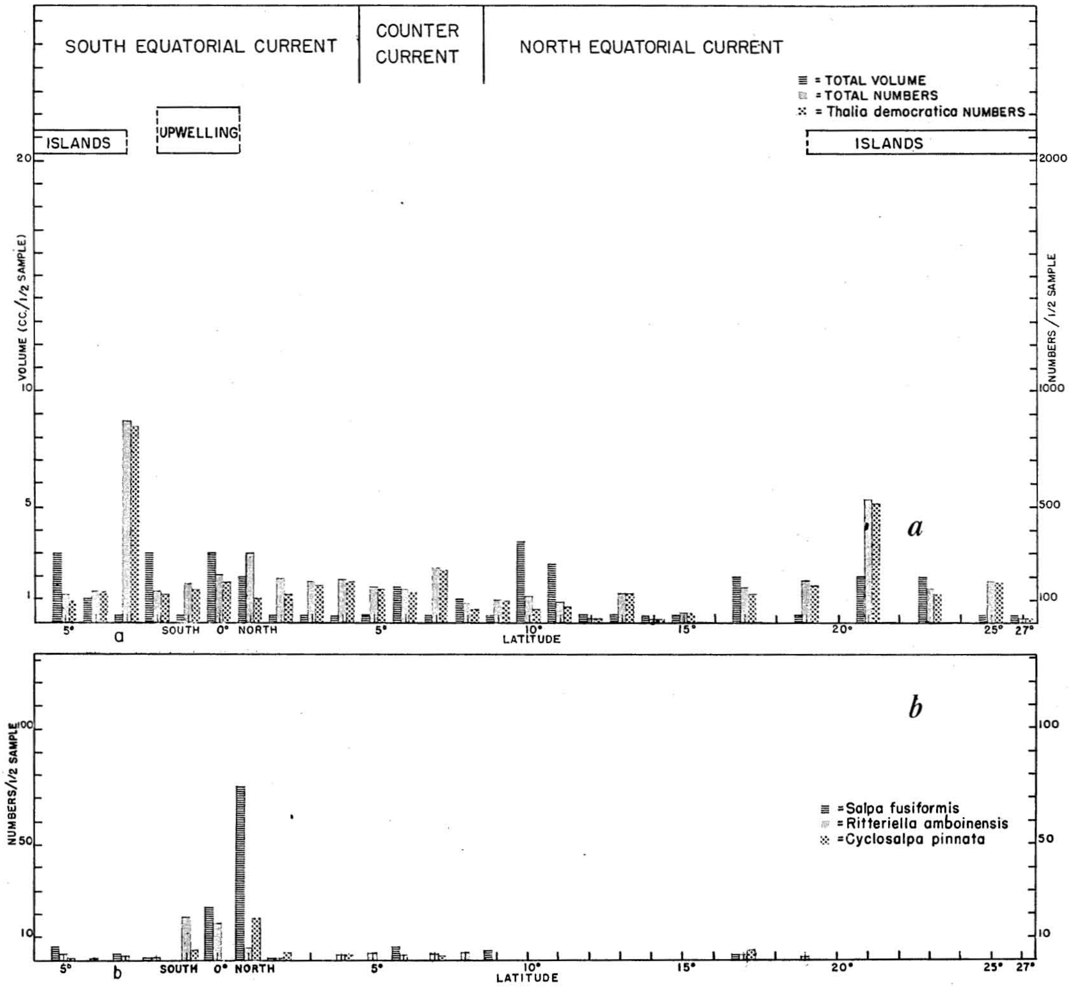


FIG. 4. Cruise 5, 172° W. longitude. *a*, Relationship of total salp volume, total salp numbers, and numbers of *Thalia democratica* to major currents, upwelling, and island masses. Limits of currents, upwelling, and islands are approximate. *b*, Relationship of the other common species, *Salpa fusiformis*, *Ritteriella amboinensis*, and *Cyclosalpa pinnata* to major factors listed in *a*.

relationship to the ecologic factors examined.

The section of cruise 8, 172° W. (Fig. 6), shows that relatively large volumes were taken in the region of upwelling and near the current margins of the Counter and North Equatorial Currents. Relatively great numbers were taken also in these regions, with a predominance of the greater numbers near the region of upwelling.

In summary, it can be stated that most of the greater volumes and numbers of salps taken on these longitudes were taken either within or near the cool enriched upwelled waters, in regions possibly influenced by current shear, or in regions in which there was a possible island influence on their abundance. The effect of temperature on salp abundance is undoubtedly only indirect within the ranges found on these cruises, inasmuch as cool non-upwelled waters contained, in general, relatively few salps except near islands. This predominance of greater volumes in regions of upwelling occurred on cruise 5, 158° and 172° W., and cruise 8, 172° W. The abundance of the salps on cruise 8, 158° W., appeared to be unrelated to upwelling, however. There appears to have been an influence of island proximity on salp abundance on cruise 5, 158° and 172° W. It apparently had no effect on the abundance at either longitude of cruise 8. The influence of shearing at current margins apparently affected salp abundance on cruise 5, 158° W., and cruise 8, 158° W. Other than these, no relationships of salps to ecologic factors can be determined from the available data.

Relative Abundance of Species

The most numerous species of salp in the POFI collections is *Thalia democratica*. In the central Pacific Ocean, therefore, the statement of Apstein (1906) that this species is the commonest salp in warm water holds true. Similarly, in the East Indies (Ihle, 1910), the Philippines (Metcalf, 1918), the Great Barrier Reef lagoon (Russell and Colman, 1935), and southeast Australia (Thompson, 1948), *T. democratica* is the commonest species found. However, it was reported by Ritter (1905) as

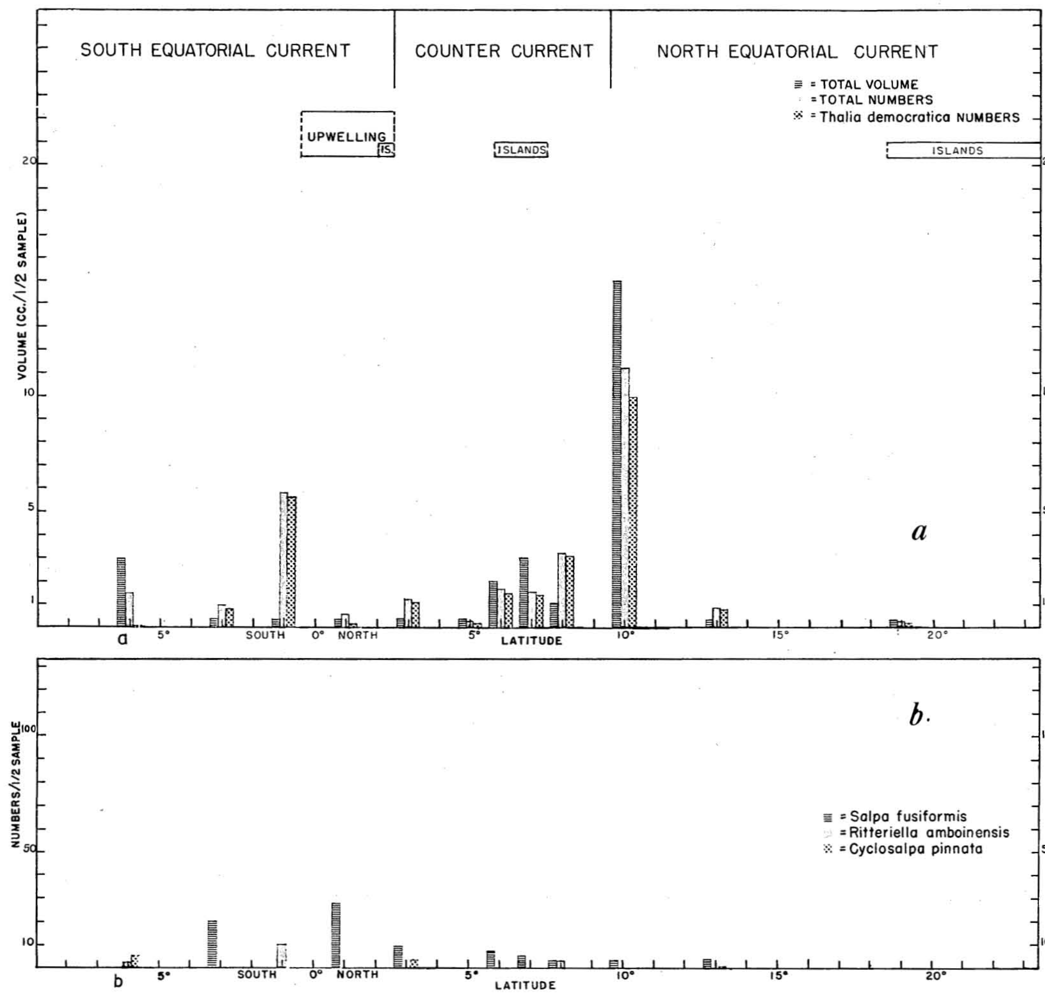


FIG. 5. Cruise 8, 158° W. longitude. *a*, Relationship of total salp volume, total salp numbers, and numbers of *Thalia democratica* to major currents, upwelling, and island masses. Limits of currents, upwelling, and islands are approximate. *b*, Relationship of the other common species, *Salpa fusiformis*, *Ritteriella amboinensis*, and *Cyclosalpa pinnata* to major factors listed in *a*.

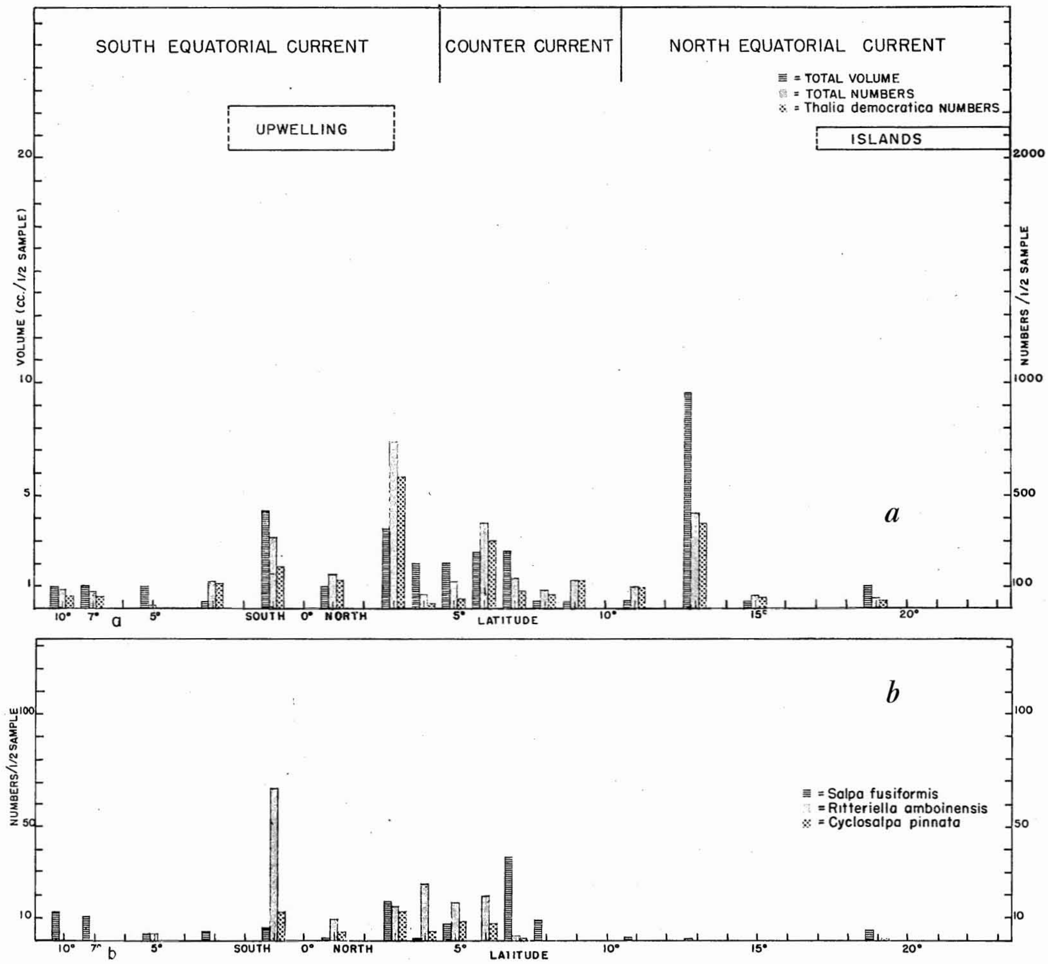


FIG. 6. Cruise 8, 172° W. longitude. *a*, Relationship of total salp volume, total salp numbers, and numbers of *Thalia democratica* to major currents, upwelling, and island masses. Limits of currents, upwelling, and islands are approximate. *b*, Relationship of the other common species, *Salpa fusiformis*, *Ritteriella amboinensis*, and *Cyclosalpa pinnata* to major factors listed in *a*.

being less abundant than *Salpa fusiformis* off the coast of California; this is perhaps a result of the lower temperatures in California waters.

RELATIVE IMPORTANCE OF DOMINANT SALP SPECIES IN THE CENTRAL PACIFIC

Frequency of occurrence by station

Cruise 5	Cruise 8
1. *Thalia democratica*	*Thalia democratica*
2. *Ritteriella amboinensis*	*Salpa fusiformis*
3. *Salpa fusiformis*	*Ritteriella amboinensis* and *Cyclosalpa pinnata*

Numerical ranking of species

1. *Thalia democratica*	*Thalia democratica*
2. *Salpa fusiformis*	*Traustedtia multitentaculata*
3. *Ritteriella amboinensis*	*Salpa fusiformis*

Frequency of dominance by volume

1. *Iasis zonaria* and *Ritteriella amboinensis*	*Ritteriella amboinensis* and *Thalia democratica*
2. *Thalia democratica*	*Salpa fusiformis*

The chief salp component by volume in the central Pacific varies irregularly at the different stations. As volume is difficult to determine precisely, especially when there are few specimens of small species, volumes were determined to the nearest cubic centimeter and the chief component species was estimated by visual inspection. In some samples no one species predominated but usually one species predominated volumetrically; the same species or a different one might predominate numerically. The chief component species by volume may be a single specimen of a large species or a few specimens of a medium sized species, which may predominate over even large numbers of smaller species such as *T. democratica*. Inasmuch as specimens larger than 5 cm. were removed from the samples before the present study, the volumetric data may be incorrect for some stations, although, as King and Demond stated, these larger specimens were infrequent.

Comparison of Salp Abundance with Total Plankton Abundance

King and Demond (1953) have reported on the total plankton of cruises 5 and 8 by volume and numbers per cubic meter of water strained. The original numerical estimates and volume determinations were made available through the courtesy of Mr. King and the salp percentages discussed here were calculated from them.

Salps comprised more than 50 per cent of total plankton by volume at only one station (50) of cruise 5 (54 per cent); the highest percentage by number made up by salps was 9.1 per cent, at station 48 of cruise 5. On cruise 8, salps amounted to more than 50 per cent of the total volume at stations 9 (58 per cent) and 101 (65 per cent); the highest percentage by number was 4.1, at station 9.

These results, combined with the numerical percentage estimates of tunicates as compared with other zooplankters by King and Demond, show that tunicates in general play a relatively small numerical role in the central Pacific plankton, but that salps in particular may attain a substantial volume as compared with other plankters. Ordinarily, however, salps play a rather minor role both volumetrically and numerically. Thompson (1942) stated, in reference to southeastern Australian waters, "Tunicates . . . comprise, next to Crustacea, the chief portion of the zooplankton," and, "Tunicates (chiefly salps) are the only other group which frequently predominates . . .," with a monthly average percentage of 25.4 as compared to 62.5 per cent for Crustacea. Thus, although the methods of capture are not strictly comparable, there is evidently a rather pronounced difference in the composition of the plankton between the central Pacific and southeastern Australian waters.

By using the methods described in Snedecor (1946, chap. 7), correlation coefficients were calculated to determine the relationship between salp numbers and zooplankton numbers (less salps) and salp volume and zooplankton volume (less salps) for cruises 5 and 8. In order to make use of salp volumes that measured less than 1 cc., such volumes were given an assumed measure of 0.5 cc. in the calculations. Neither correlation coefficient was significant for numbers or volumes of these cruises. From the evidence based on these cruises, then, there is no significant mutual relationship between salp and zooplankton numbers or volumes.

Comparison of Salp Abundance in the Central Pacific with Other Regions of the Pacific

It is impossible to make accurate quantitative comparisons between the plankton of different regions unless equipment and methods of capture are standardized. Unfortunately such optimal conditions have never been met. Nevertheless, as salps are relatively large animals and thus are taken by the commonly used nets, an attempt is made here to compare the salps of the central Pacific to those of the Great Barrier Reef lagoon as reported upon by Russell and Colman (1931, 1935), the only Pacific investigators who have listed salps and other zooplankters by station and numerical frequency. Such a comparison is made more reliable by the fact that Russell and Colman used a 1-meter coarse international silk townet, which has an approximate mesh width of 0.42 mm.; the 1-meter nets used by POFI have a mesh width of 0.65 mm. (King and Demond, 1953). In addition, Russell and Colman towed their nets obliquely at each station for approximately a half hour, as was done for the POFI collections.

The chief difficulties with such a comparison are: (1) the amount of water strained was not computed by Russell and Colman and thus estimates of relative abundance of the plankton are only approximate; (2) volumes of the different groups of plankters were not determined for the Great Barrier Reef collections and thus, number of organisms, a relatively poor measure, offers the only means of comparison; and (3) the depth to which the POFI tows were made was approximately 200 meters, whereas those of the Great Barrier Reef Expedition were made to approximately 30 meters.

Russell and Colman (1935) listed the tunicates which occurred in oblique tows with the 1-meter coarse silk townet by species, reproductive form, and numerical frequency at 59 stations of the Great Barrier Reef lagoon. Comparison of these data with the data from the central Pacific reveals some striking differences. Only 6 salp species (4 with the coarse silk townet) were captured in the Barrier Reef lagoon, whereas 19 (16 on cruises 5 and 8) were captured in the central Pacific. *Thalia democratica* was by far the most numerous and frequently occurring species (80,987 specimens at 39 Barrier Reef stations), as it also was in the central Pacific. The fact, however, that *T. democratica* was lacking from fully 20 of the 59 Barrier Reef stations is surprising when compared with the POFI collections, where it was absent at only 2 out of 81 stations examined. In addition, this species was occasionally much more numerous in the Barrier Reef lagoon than in the central Pacific (maximum numbers at one station of 17,000 and 3,440, respectively).

The other species found in the Great Barrier Reef lagoon rank among the relatively less common and infrequently occurring species in the central Pacific: *Brooksia rostrata* occurred in the Barrier Reef at 10 stations out of 59 (117 specimens), whereas in the POFI collections, it occurred at 24 stations out of 81 (259 specimens); 111 specimens of *Pegea confoederata* occurred at 8 stations out of 59 in the Barrier Reef, whereas 185 specimens occurred at 12 stations out of 81 in the central Pacific; *Weelia cylindrica* occurred at 13 stations (53 specimens) out of 59 from the Great Barrier Reef, whereas it occurred at 23 stations out of the 81 POFI collections examined (259 specimens). With the exception of *T. democratica*, the most numerous and frequently occurring species in the POFI collections, *Salpa fusiformis*, *Ritteriella amboinensis*, *Cyclosalpa pinnata*, and *Traustedtia multitentaculata*, did not occur at all in the Great Barrier Reef collections. All of these species, however, occur in oceanic Australian waters (Thompson, 1948).

Another striking difference between the collections from the Great Barrier Reef and those from the central Pacific is the large number of stations from the former at which no salps occurred (15 out of the 59 listed), whereas in the POFI collections, salps occurred at all 81 stations examined. In addition to the 59 tunicate-containing stations listed by Russell and Colman, there were 9 other collections made, which contained no tunicates.

On examining their data, another difference becomes evident; that is, a maximum of 17,003 specimens of salps (almost all *T. democratica*) was captured at one station, whereas the maximum number at any one station in the POFI collections was 3,864 (chiefly *T. democratica*). The maximum number of salp species taken with the coarse silk townet at any one station in the Great Barrier Reef, however, was only 4; in the POFI collections, the maximum number of species at any one station was 9, more than twice the maximum number from the Barrier Reef.

In summary, then, bearing in mind the difficulties of quantitative comparisons, the chief differences between the Salpidae of the Great Barrier Reef lagoon and of the central Pacific Ocean, based on limited captures, are as follows: (1) the numbers of species found are much fewer as a whole in the Great Barrier Reef than in the central Pacific; (2) the maximum numbers of species present at any one station are much fewer in the Barrier Reef than in the central Pacific; (3) the numbers of individuals at any one station are often much greater in the Barrier Reef than in the central Pacific; (4) salps are more highly sporadic in distribution in the Barrier Reef than in the central Pacific, even being entirely absent from many stations, whereas they are present in all the POFI collections; (5) the most numerous and frequently occurring species, *T. democratica*, is the same in the two areas, but the species ranking next numerically and in frequency of occurrence are entirely different. Species other than *T. democratica* found in the Barrier Reef lagoon are relatively sparse and infrequent in the central Pacific collections, while the ranking species, other than *T. democratica*, of the central Pacific are wholly lacking from the Barrier Reef collections, although they occur offshore in the Australian region. These differences probably reflect chiefly the widely differing ecologic conditions between a neritic and an oceanic environment.

DISTRIBUTION OF SALPS

Geographic Distribution

Almost all investigators of planktonic animals have concurred with Giesbrecht's observation that, ". . . the epipelagic high-oceanic fauna may be divided into three main zoogeographical regions: a warm-water and a northern and a southern cold-water zone" (Ekman, 1953). This is true of the Salpidae except for the fact that there are no species confined to northern cold water. Therefore, it appears that water temperature is the primary limiting factor in the distribution of salps.

The majority of salps are cosmopolitan warm water plankters, although they may be carried into high latitudes from time to time. Only *Ihlea magalhanica*, *Thalia longicauda*, *Helicosalpa komaii*, and *Cyclosalpa strongylenteron* have been reported as restricted to certain oceanic regions. According to Apstein (1894, 1906) and Thompson (1948), *I. magalhanica* is restricted to the cool waters of the southern hemisphere; this is also true of *T. longicauda* according to Apstein, but Sewell (1953) reported one specimen from the northern Arabian Sea. *H. komaii* has been reported only from Japan (Komai, 1932) and the central Pacific (Yount, 1954), and *C. strongylenteron* only from the eastern Pacific (Berner, 1955), but both probably will be found to occur in the Indian and Atlantic oceans as well. Table 1 lists salp distribution by species as reported by Pacific investigators.

The remaining species of salps have been reported from the Atlantic, Indian, and Pacific oceans, except for *Ihlea punctata*, which has not yet been found in the Indian Ocean although it probably occurs there. Even the continents of South America and Africa do not prevent the transport of salps from one ocean to another, inasmuch as Herdman (1888) reported *Iasis zonaria* and Apstein (1906) listed *Salpa maxima* and *S. fusiformis* from the Straits of Magellan, and Apstein (1906) showed that *S. maxima*, *S. fusiformis*, *Metcalfina hexagona*, *Thalia democratica*, *T. longicauda*, *Pegea confoederata*, *Ia. zonaria*, and, of course, *Ih. magalhanica* had been captured at the region of the Cape of Good Hope or in more southerly waters. Salps are carried far into northern waters also (see Ihle, 1935), but probably cannot be carried alive into the Arctic Ocean.

With the exception of the four species mentioned above, then, it can be stated that the Salpidae is a family of cosmopolitan

TABLE 1
DISTRIBUTION OF SPECIES OF SALPIDAE (EXCEPT *I. magalhanica* AND *T. longicauda*)

SPECIES	ATLANTIC	INDIAN	JAPAN	PHILIPPINES	EAST INDIES	AUSTRALIA	N. E. PACIFIC	CENTRAL PACIFIC	EAST PACIFIC
Cyclosalpa pinnata	+	+	+	+	+	+	+	+	–
C. affinis	+	+	+	–	–	+	+	+	+
C. floridana	+	+	–	–	+	+	–	+	–
C. bakeri	+	+	+	+	+	+	+	+	+
C. strongylenteron	–	–	–	–	–	–	+	–	+
Helicosalpa virgula	+	+	–	–	–	+	–	+	–
H. Komaii	–	–	+	–	–	–	–	+	–
Brooksia rostrata	+	+	–	+	+	+	–	+	–
Ihlea punctata	+	–	+	–	+	–	–	+	–
Salpa fusiformis	+	+	+	+	+	+	+	+	+
S. maxima	+	+	+	+	–	+	+	+	+
Weelia cylindrica	+	+	+	+	+	+	+	+	+
Ritteriella amboinensis	+	+	+	+	+	+	–	+	–
R. picteti	+	+	+	–	+	+	+	+	–
Metcalfina hexagona	+	+	–	+	+	+	–	+	+
Thetys vagina	+	+	+	+	+	+	+	+	+
Pegea confoederata	+	+	+	+	+	+	+	+	+
Traustedtia multitentaculata	+	+	+	–	+	+	–	+	–
Thalia democratica	+	+	+	+	+	+	+	+	–
Iasis zonaria	+	+	+	+	+	+	+	+	+

oceanic plankton organisms in the circumglobal warm water zone.

Seasonal, Latitudinal, and Longitudinal Variation

Cruise 5 was carried out during June, July, and August of 1950, the northern summer, and cruise 8 was carried out during January, February, and March of 1951, the northern winter. A comparison of the two cruises should reveal seasonal variations, if any are present; therefore, an analysis of variance was calculated to determine seasonal differences. Longitudes and latitudes were analyzed simultaneously with seasons by the method described by Snedecor (1946: 304–309). Volumes were used as the variate rather than numbers, as volume is a better measure of the organic material in a plankton tow.

King and Demond (1953), who studied the total zooplankton volumes on cruises 5 and 8, demonstrated no significant first- and second-order interactions and no significant differences between longitudinal means, but did demonstrate significant differences between the means for seasons and for latitudes: No significant differences for the salp volumes, however, were demonstrated between either of the means for longitudes, for seasons, or for latitudes. Neither are there significant differences in the first- and second-order interactions, except that between longitudes and seasons. Therefore, there is probably ($P = 0.03$) an interaction between longitudes and seasons that produced the observed differences in volumes of salps at the 11 compared latitudes. I am unable to offer any conjectures to explain this interaction; it must be borne in mind, however, that the analysis is based on a few samples and that the variation in distribution of plankters, as well as the limited sampling by towing, could easily distort the resultant picture. This analysis supports the conclusion noted earlier under the comparison of volumes of salps and of the remaining zooplankton, i.e., that variation in salp volume does not necessarily relate to that of the total zooplankton, and was very different in the samples studied.

Relationship of Salps to Oceanic Currents

Comparison of the species at each station of cruises 5 and 8 (at the latitudes of Figs. 1 and 2, exactly listed by King and Demond, 1953), with the current system of the central Pacific (Cromwell, 1954) showed that there were only three species of salps found in but one current on these cruises. On cruise 5, 172° W., for example, *Cyclosalpa bakeri* and *Ihlea punctata* were found only in the South Equatorial Current. Examination of the distribution of these species on other longitudes and cruises, however, shows that they were found at some station in all other currents as well. This is true also of most other species, as they occurred in one longitude or another or on one cruise or another in all of the principal currents. Only three species were restricted in the central Pacific, *Cyclosalpa affinis*, *C. floridana*, and *Metcalfina hexagona*, the first and last of which occurred in only one current; *C. floridana* occurred in only two currents. *C. affinis* occurred at no other station of the two cruises and only three specimens were captured. It is thus an uncommon species in the POFI collections studied, and probably cannot be considered as an indicator of this current. *M. hexagona* was also captured at only one station on only one cruise, but occurred in fair numbers (43 specimens). On other cruises, however, it is not an extremely rare species, since in the collections of animals larger than 5 cm. from all POFI cruises, it occurs in at least five samples. It cannot be considered an indicator species, then, on the basis of only one record on one cruise, particularly since only 32 stations of cruise 8 were examined. *C. floridana* was also a relatively uncommon species on these cruises and thus cannot be regarded as an indicator species.

Ihlea magalhanica, a species not found in the POFI collections, has been considered a probable indicator species of colder water advancing northerly in the Australian area (Thompson, 1948). Thompson stated that *Ih. magalhanica* "is one of the salp species which has a low tolerance of warm water conditions," and that it "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." In the same report, however, he stated, "there is . . . no evidence of a genuine cold water influence, even in Tasmanian waters, although in the latter region species which are characteristic of warm-temperature waters as well as of circumtropical waters are those most usually found (e.g., *Ihlea magalhanica*, *Iasis zonaria* and *Thetys vagina*)." *Ih. magalhanica* was earlier reported by Apstein (1894, 1906) in the Antarctic, westerly and southwesterly of the southern point of Africa, and in the Straits of Magellan, in water with a temperature range from 0° to 12.3° C. Thompson (1948), however, reported the temperature range of this species as between 11.6° and 22.25° C. This species, therefore, should perhaps be regarded as a eurythermal, rather than a stenothermal, cool water form and its usefulness as an indicator of cold water currents perhaps is much less than was thought previously. Its presence in water with a temperature of 22.25° C. may be exceptional, i.e., it may have been transported into such water but may not be long viable there, or the animal(s) may have been actually in a deep cool layer of water at this station. Thompson did not explain the situation, however.

Therefore, it can be stated that all salps captured on cruises 5 and 8 can be expected to occur in all currents in warm latitudes and that they are not satisfactory indicator species for these latitudes. Three uncommon species might possibly be true indicator species, but this is doubtful.

ECOLOGICAL NICHE OF SALPS

When one contemplates niches in the marine plankton community, it becomes clear that there are relatively fewer niches in the plankton than there are in the benthos or in land communities ("The 'niche' of an animal means its place in the biotic environment, *its* *relations to food and enemies,*" Elton, 1927: 64). For example, in the warm water epipelagic zone, the species are remarkably similar the world over (this is true of salps and it is undoubtedly true of other plankters as well); but even an oceanic island, such as Oahu for example, doubtlessly possesses many times more species of organisms than the plankton of the whole, vast epipelagic zone in the warm water belt of the world. This observation, I think, reflects the general paucity of niches and habitats in the pelagic oceanic environment, due most likely to the remarkable uniformity of the physical conditions and to the lack of shelter there.

The Salpidae is one of the many groups of planktonic filter feeders; salps feed by straining the water which passes through their body cavities by means of mucus strings secreted chiefly from the endostyle (see Ihle, 1935, 1937–39). Notwithstanding differences in structural and physiological mechanisms associated with filter feeders, they catch and consume, in general, the same organisms as other pelagic tunicates (pyrosomids, doliolids, and to some extent appendicularians), some pteropods, some copepods, and perhaps other constituents of the plankton, since the food of all these organisms is captured by simply filtering the water. It has long been known that salps are not selective feeders and that methods and mechanisms for feeding are similar in all species thus far studied (see Ihle, 1935, 1937–39).

In order, then, to attempt a segregation of the niches of the various species of salps, an analysis of the gut contents of all species reported here was undertaken, and observations were made as to their probable predators. Various salp species were chosen from different latitudes, longitudes, and cruises in order to have a respresentative sample. This resulted in the following observations: the food of all specimens and species of salps is remarkably similar throughout the area studied; and the food of all salp species within any one plankton sample is the same.

SUMMARY OF THE RESULTS OF THE GUT CONTENT ANALYSES

very common food. .	unidentified matter
	diatoms
	dinoflagellates
common food.	silicoflagellates
	radiolarians
	coccolithophores
	foraminiferans
rare food.	small crustaceans (chiefly copepods)
	gastropod larvae
	pteropods
	annelids
	fish eggs

Enemies of salps under natural conditions are unknown. Observations that may provide a clue on this situation, however, have been made in the plankton samples. There is a certain amount of conjecture in such deductions because carnivorous animals can be expected to bite whatever is near them during the death struggle after formalin is added to a plankton sample. Nevertheless, animals that contain salps in their digestive tracts or that hold to salps in the preservative may be their enemies in nature. Obviously, a chaetognath could be predaceous on *Thalia democratica* but not on *Thetys vagina* except in its young stage. The following animal types have been observed holding onto salps in preserved plankton tows: chaetognaths, heteropods, coelenterates, and crustacea (chiefly copepods and hyperiid amphipods). No planktonic animals have been observed to contain salps in their guts, but special study was not performed with this object in mind. Thompson (1948: 160) reported *Salpa fusiformis* from stomachs of blue cod from New Zealand, and Reintjes and King (1953) reported *Pyrosoma* sp., unidentified salps, and unidentified tunicates other than these in the gut contents of yellowfin tuna (*Neothunnus macropterus*). Fraser (1949) reported *I. asymmetrica* (= *I. punctata*) and *Dolioletta gegenbauri* from a herring stomach, and that salps were reported as part of the food of the pelagic turtle, *Thalassochelys caretta*. I have recently identified five specimens of *Thalia democratica* agg. from the gut contents of a fish, *Chaetodon unimaculata*, taken by rotenone poison off Honolulu at a depth of about 25 feet. This fish contained many appendicularians also, probably of the genus *Oikopleura*. Other than this, no information is available as to the enemies of salps.

Because there is no apparent selection of food, and because the food, feeding methods, and mechanisms are similar in all species of salps, and because enemies are evidently similar, all salp species appear to occupy similar niches (with some slight differences between salps of different sizes in their ability to handle the larger food organisms). Inasmuch as many species of salps have been found together in one plankton tow (up to 9 in the POFI collections studied), and all species in a plankton tow can be assumed to be subject to at least approximately the same enemies and to the same environmental conditions, it can be stated that all salps apparently occupy similar niches simultaneously, and are, for all practical purposes, ecological equivalents. This statement doubtless applies to many other plankters as well as to salps: Any one niche in the plankton community of the epipelagic zone of tropic oceanic waters may be occupied simultaneously by many species. To illustrate, a few specimens of doliolids and pyrosomids have been subjected to a gut content analysis, and these animals also contained generally the same food organisms as the salps. Appendicularians, although to some extent feeding on similar food as other planktonic tunicates, are probably more restricted in the type of food they can handle as a result of their highly modified food-catching mechanisms, and are thus probably limited in their equivalence with other pelagic tunicates. It is probable that predaceous plankters such as chaetognaths, heteropods, coelenterates, and some crustacea found in tropic epipelagic waters also occupy similar niches simultaneously.

Marshall and Orr (1953) briefly discussed the concept of the niche (including the concept of habitat in the same term) in regard to the plankton community and pointed out that ". . . it is at first sight hard to understand how different ecological niches can be available in a medium so constant as sea water." They suggested that differences in niches among plankters may be found in the different foods on which the plankters depend. Such a suggestion may be applicable to plankters found in coastal and temperate waters, but for tropic oceanic waters it seems scarcely applicable, at least to the salps and undoubtedly also to many other plankton animals. To be certain of this niche equivalence, it would be desirable to know the vertical distribution of the captured animals, but the tows studied cannot furnish such information, as they were made with an open net. Conjectures have been made as to the causes and results of this apparent niche equivalence of many species, but they are not included in this report. They have resulted in a study of species variety in Silver Springs, Florida, in which factors controlling the numbers of species are discussed (Yount, 1956).

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