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Zoogeography and speciation in the Salpidae (Tunicata, Thaliacea)

R. W. M. VAN SOEST

ABSTRACT

This paper represents a general study of two major phenomena in the taxonomy of the lower taxa of the Salpidae and their bearing on theories about the origin of the recent species. Arguments are presented that point strongly to a specific status for closely related forms previously described as infraspecific by most authors. Latitudinal-clinal variation, reported for the first time in salps in a previous paper of the present author, is now demonstrated to be a uniform trend in all species with a wide distribution into temperate waters. Some indications are found that support the assumption that the clinal forms represent separate populations with a small degree of genetic difference. *Thalia democratica* (Forskål, 1775) is divided into two formae, forma *democratica*, distributed over the whole of the Atlantic and the subtropical and temperate parts of the Indo-Pacific, and forma *indopacifica* nov., confined to the tropical parts of the Indo-Pacific. On the basis of the species distribution and the occurrence of clinal variation the surface waters of the world oceans are divided into 11 major biogeographic regions, largely conforming to similar divisions made on the basis of other holoplanktonic groups. Finally postulations are made about the most likely mode of speciation of the lower taxa in the Salpidae. Climatic deterioration and lowering of the sea surface temperatures during glaciations of the past four million years are thought to have caused isolation of salp populations in the Atlantic Ocean. This isolation presumably resulted in the present species diversity.

1. INTRODUCTION

In the past four years the present author studied the taxonomy and distribution of the Salpidae (van Soest, 1972, 1973a, 1973b, 1974a, 1974b, 1975), a group of holoplanktonic, for the most part truly oceanic Tunicata. The number of taxa known previously in this family (and order) (cf. Yount, 1954; Berner, 1955; Foxton, 1961, 1971; Borgelt, 1968; Kashkina, 1973) was raised from about 35 to 44 at present. The taxa were redescribed and their distribution more exactly defined. The present author has studied specimens of all

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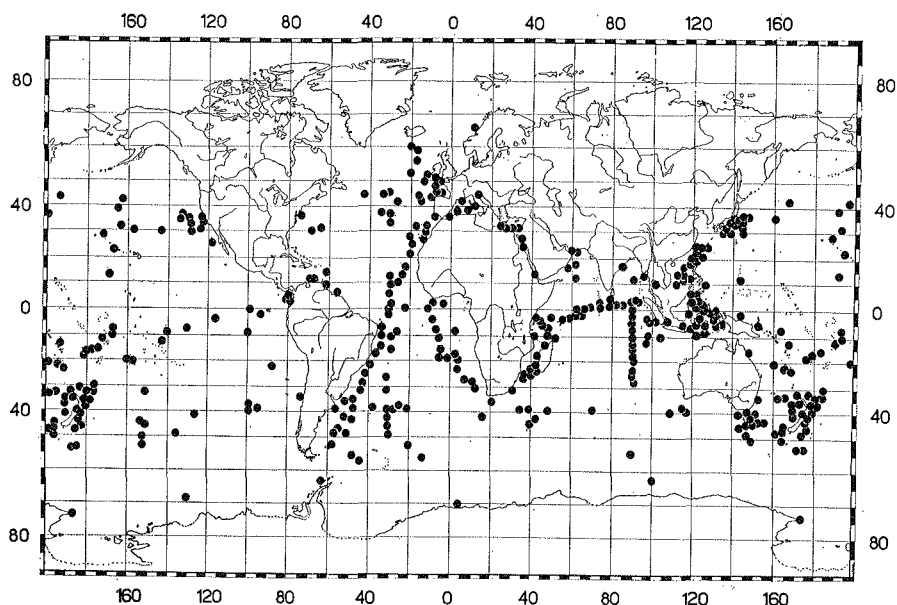


FIG 1. Localities from which samples were studied.

known taxa with the exception of *Helicosalpa younti* Kashkina, 1973, of which only two solitary specimens are known. Although several species are incompletely known, it is felt with some confidence that a general study of the major phenomena in the taxonomy of the lower taxa can be made and that some postulations about the process of speciation of the lower taxa are in order.

2. MATERIAL §

The present study is based on material cited in previous papers. It concerns primarily samples collected by various oceanic expeditions (Dana Expeditions, Galathea Expedition, Siboga Expedition, Discovery Expeditions, Great Barrier Reef Expedition, John Murray Expedition, CICAR-cruises, ACRE-cruises, U.S. Smithsonian Institution Mediterranean Cruises), and furthermore a number of incidental samples. The station numbers and data will not be repeated here, but all localities from which material was studied are represented in the chart of fig. 1.

3. ACKNOWLEDGEMENTS

Friendly cooperation has been received from various ship crews, musea and institutions in the sampling, loan and donation of the material. All persons concerned are thanked again, without mentioning anyone in particular.

A special word of indebtedness is due to Dr. S. van der Spoel, who suggested this study, advised and helped in many ways, discussed and critically revised this and previous papers. Discussions about taxonomy and speciation in holoplanktonic zooplankton, held with Mrs. Drs. A. C. Pierrot and Dr.

P. Foxton contributed to the views taken by the present author on these subjects in the case of the Salpidae.

Mr. J. Zaagman prepared some of the figures.

4. THE OCCURRENCE AND STATUS OF CLOSELY RELATED TAXA

Until 75 years ago the Salpidae were considered generally as a group of neatly defined monotypical species having for the most part a cosmopolitan warm water distribution. Metcalf (1918), in his monograph of the Salpidae focussed attention on deviating specimens, varieties and subspecies. In subsequent decades a lot of suppressed subspecies were revived and a fair number of new ones were described. The status of these "subspecies" was only cursorily argued. The general thought apparently was typological: they differed so slightly from the already established species, and resembled these so closely that they could not be anything else but conspecific. A number of the leading authors in the past decades attempted to suppress these "subspecies", stating that they were merely extremes of a rather wide variation, or juvenile c.q. senile forms (Sewell, 1926, 1953; Thompson, 1948; Yount, 1954). Foxton (1961, 1971) studied some of these "subspecies"-assemblages (*Salpa fusiformis* Cuvier, 1804, and its relatives, *Ihlea magalhanica* (Apstein, 1894) and its relative) very thoroughly, and concluded that they represent clearly defined species, although the observed differences with previously established species were small. In earlier studies of the present author an inventory was made of all the described Salp "subspecies" or varieties, and they almost invariably proved to be good taxa. Next to these, seven closely related taxa have been newly described. A survey of the closely related taxa is given in Table I. In only a few instances reported subspecies or species were found to be based on faulty observations and had to be synonymized.

TABLE I. Closely related (partly) sympatric species.

<i>Cyclosalpa pinnata</i> -group:	<i>Cyclosalpa pinnata</i>
	<i>Cyclosalpa polae</i>
	<i>Cyclosalpa sewelli</i>
	<i>Cyclosalpa quadriluminis</i>
<i>Cyclosalpa bakeri</i> - <i>Cyclosalpa foxtoni</i>	
<i>Cyclosalpa affinis</i> - <i>Cyclosalpa danae</i>	
<i>Helicosalpa virgula</i> - <i>Helicosalpa younti</i>	
<i>Brooksia rostrata</i> - <i>Brooksia bernerii</i>	
<i>Ritteriella retracta</i> - <i>Ritteriella picteti</i>	
<i>Salpa aspera</i> - <i>Salpa younti</i>	
<i>Salpa maxima</i> - <i>Salpa tuberculata</i>	
<i>Pegea confoederata</i> - <i>Pegea bicaudata</i>	
<i>Thalia democratica</i> -group:	<i>Thalia democratica</i>
	<i>Thalia cicar</i>
	<i>Thalia orientalis</i>
	<i>Thalia rhomboides</i>
	<i>Thalia rhinoceros</i>
	(<i>Thalia sibogae</i>)

The occurrence of closely related sympatric (or partly sympatric) taxa seems an almost universal feature in the Salpidae, as more than half of the “distant” species have one or more close relatives. In contrast to closely related species, “distant” species may be defined as congeneric species differing clearly and strongly in their morphological characters, for example *Salpa maxima* Forskål, 1775, and *Salpa fusiformis* Cuvier, 1804, or *Thalia democratica* (Forskål, 1755) and *Thalia longicauda* (Quoy & Gaimard, 1824), etc. In previous studies of the present author the closely related sympatric taxa have been treated as separate species. The arguments for their specific status as opposed to intraspecific status are given here.

4.1. *The presence of several small but clearly defined differences*

All the described close relatives differ in at least two, but up to five characters. These characters include in the different genera the number of muscle fibres (almost all taxa), the presence, number and position of luminous organs (subfamily Cyclosalpinae, cf. van Soest, 1974a, 1975), the shape of the dorsal tubercle (subfamily Cyclosalpinae and genus *Salpa*, cf. van Soest, 1973b, 1974a, 1974b), the absence, presence or measure of echinations of the test (genus *Salpa*, genus *Thalia*, cf. van Soest, 1973a, 1973b, 1974b), the absence, presence or shape of various test projections (genus *Salpa*, genus *Thalia*, genus *Pegea*, cf. van Soest, 1973a, 1973b, 1974b, 1975), the number of body muscles (genus *Ritteriella*, cf. van Soest, 1974b), the dorsal arrangement of the body muscles (almost all taxa), and the arrangement of the atrial musculature (genus *Pegea*, cf. van Soest, 1974b).

4.2. *The absence of intermediates*

Although at one time (van Soest, 1973a) a presumed hybrid specimen of two closely related taxa has been reported (*Thalia democratica* x *Thalia cicar* van Soest, 1973), this was corrected at a later date (van Soest, 1975). The presumed hybrid specimen appeared to belong to a new taxon, described as *Thalia rhinoceros* van Soest, 1975. Some problems still exist on the identity of eastern Pacific specimens of *Salpa younti* van Soest, 1973, in view of their close similarity to *Salpa aspera* Chamisso, 1819. This has to be re-examined. In all other cases of closely related species no “hybrids” or intermediates were found.

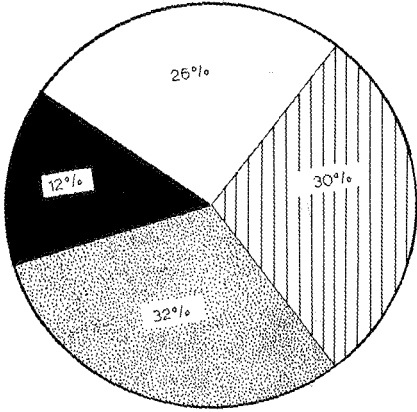
4.3. *True sympatric occurrence*

4.3.1. *Shared horizontal distributions:*

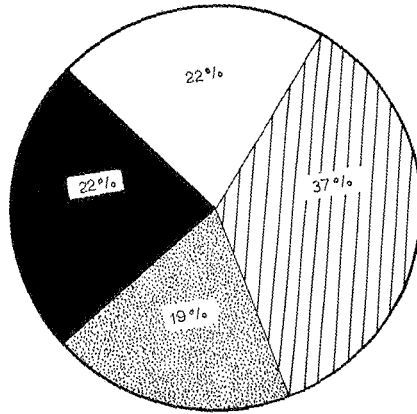
From previous papers of the present author it is clear that all closely related

FIG. 2. Schematic representation of the sympatric occurrence of members of the *Thalia democratica*-group in Indo-Pacific waters. For each of the species the percentage of occurrence in the same samples without (white segment), with one (hatched segment), with two (punctuated segment) and with three (black segment) other members of the group is given.

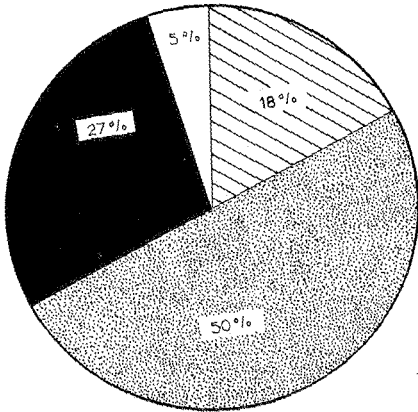
T. democratica



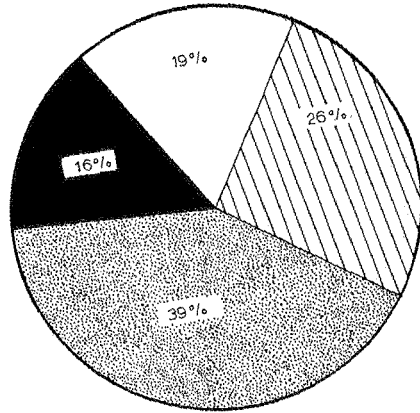
T. orientalis



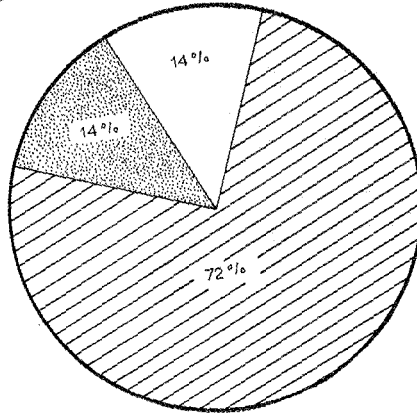
T. cicar



T. rhomboides



T. rhinoceros



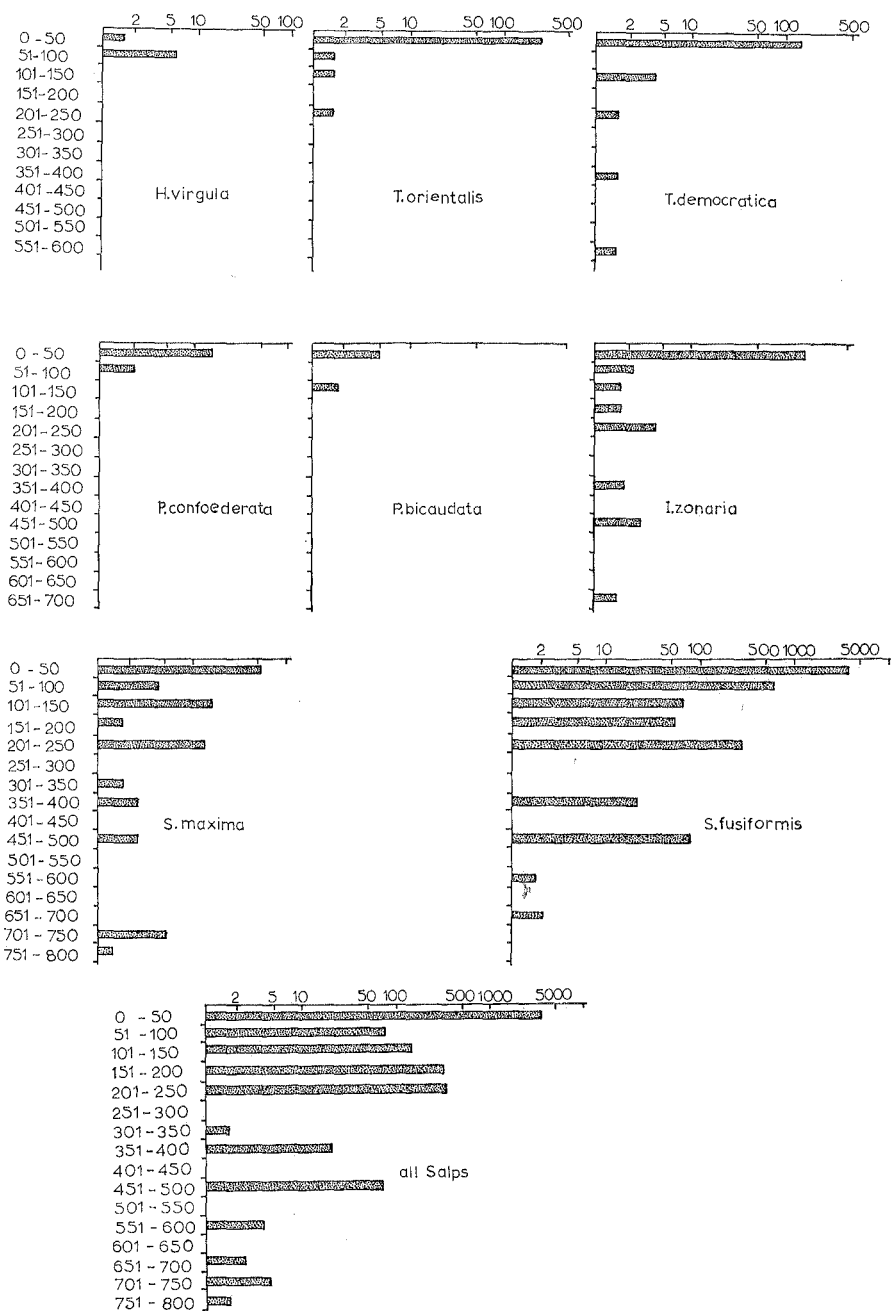


FIG. 3. Vertical distribution of 8 species of salps in the western Mediterranean (US-S1 Med. 1970 Cruise 1; 37° N, 01° E, approximately). Horizontal axis: mean numbers of specimens per sample (Logarithmic scale), vertical axis: depth in metres.

species have either their whole horizontal range in common, or a large part of it (Indo-Pacific area). It might still be possible that within this common range the species occupy different subranges, for example one species could be adapted to current systems while its close relative could prefer halostatic areas. To show that this is unlikely an example is given in fig. 2 of the sympatry of the species of the *Thalia democratica*-group (cf. van Soest, 1973a) in Indo-Pacific samples. For each species (excepting the rare and possibly neritic species *Thalia sibogae* van Soest, 1973) the percentage of occurrence in the same sample with one, two or three other members of the *Thalia democratica*-group is given in a schematic representation. From fig. 2 it is quite clear that common occurrence in a small area of two or more closely related *Thalia* species is the rule rather than an exception. Likewise, closely related species of other genera have frequently been found to occur in the same samples, as is apparent from table II.

TABLE II. Closely related species found occurring in the same samples:

<i>Cyclosalpa polae</i> - <i>C. sewelli</i> - <i>C. quadriluminis</i>
<i>Ritteriella retracta</i> - <i>R. picteti</i>
<i>Cyclosalpa bakeri</i> - <i>C. foxtoni</i>
<i>Cyclosalpa affinis</i> - <i>C. danae</i>
<i>Brooksia rostrata</i> - <i>B. bernerii</i>
<i>Salpa maxima</i> - <i>S. tuberculata</i>
<i>Salpa aspera</i> - <i>S. younti</i>
<i>Thalia democratica</i> - <i>T. cicar</i> - <i>T. orientalis</i> - <i>T. rhinoceros</i> - <i>T. rhomboides</i>

4.3.2. Shared vertical distributions:

Most of the samples studied were captured by conventional, oblique hauls of nets without closing devices. This means that those samples may have contained specimens captured at various depths, possibly from 3000 m upwards in the deepest hauls. This creates some uncertainty about the true sympatric occurrence of taxa present in the same sample, as different infraspecific populations living at different vertical strata are known in some zooplankton groups. In general it seems unlikely that salps as typical "grazing" animals have real deep water populations. Their way of foraging is simply filling themselves with sea water and filtering organic particles (the most important part of which is phytoplankton) out of it. At depths below the photic zone this seems an uneconomical feeding technique, feeding consequently will be only effective in the photic zone. That salps are in general distributed in the surface layers is illustrated by a collection of discrete depth samples from the western Mediterranean (United States Smithsonian Institution Mediterranean Cruises). The vertical distribution of the species present is pictured in fig. 3. Another series of discrete depth samples has been provided by the Ocean Acre Project near Bermuda. From these samples the vertical range of the species present has been assessed. The results represented in fig. 4, show that almost all species occurring in the Bermuda area, are known from the upper 50 m, though extreme ranges vary. By making use of only the surface hauls

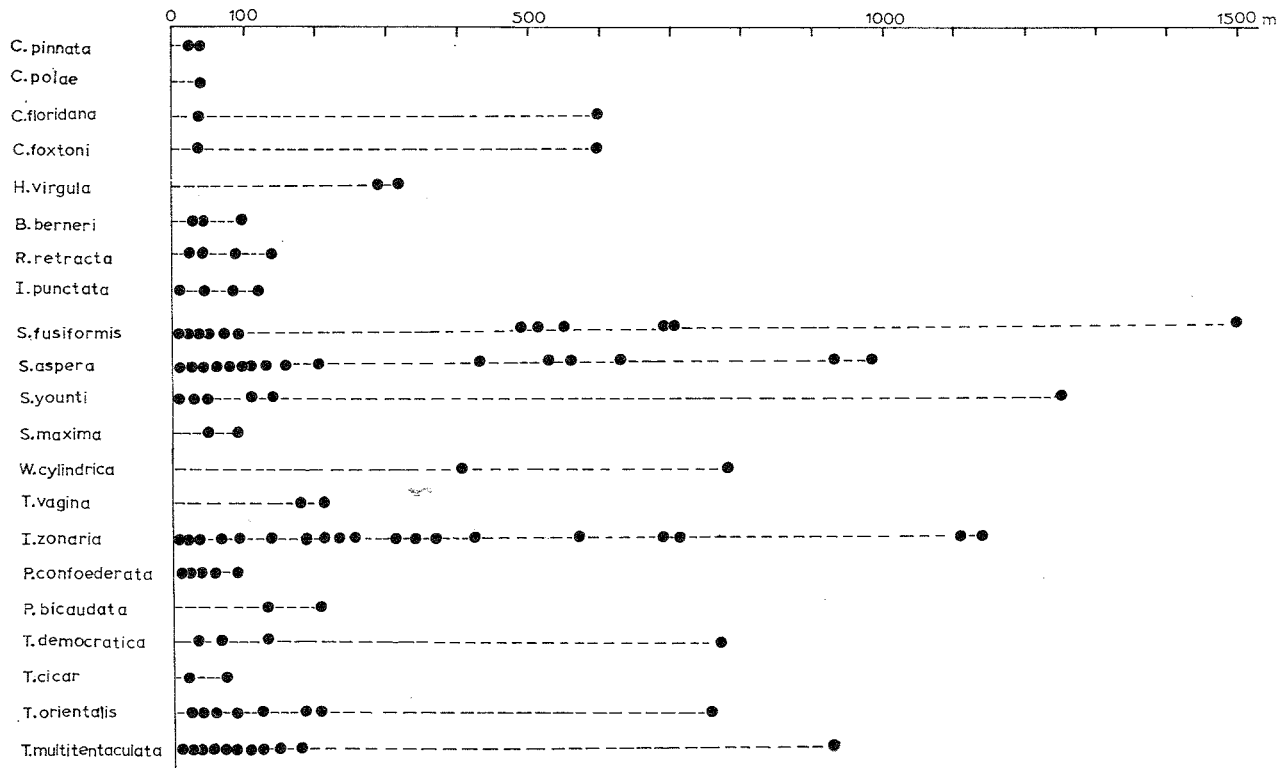


FIG. 4. Depth occurrence of 21 species of salps in the Bermuda area (Ocean Acre Program 1972). Horizontal axis: depth in metres.

(not below 50 m) made in the Indo-Pacific area and from literature data it could be established that this is applicable to all known salp species. Excepting the rare species *Helicosalpa younti* (holotype known from 400 m; of the only other specimen, mentioned by Yount (1954) the depth of capture is not given), *Helicosalpa komaii* (Ihle & Ihle-Landenberg, 1926) (literature data give no depths; one Dana sample containing this species originated from about 150 m), and *Cyclosalpa strongylenteron* Berner, 1955 (Berner gives no depth data), all other species are known from the upper 50 m. In the case of the two Indo-Pacific forms, differing in the number of muscle fibres, of both *Salpa aspera* and *Ritteriella retracta* (Ritter, 1906), which might possibly prove to be separate species (cf. van Soest, 1974b), it has been found that all occur in the surface layer, too.

The frequently reported occurrence of various species at great depths (e.g. *Salpa* spec. at 6000 m, photographed by Caldwell, 1966), must be considered with the greatest reserve. Not only is contamination of deeper samples by specimens from the upper strata likely to occur, even in discrete sampling, the capture of sinking dead salp specimens may confuse the picture of vertical distribution. A striking example is still the old experiment of Moseley (1892: 505) on board the "Challenger":

"I took a dead *Salpa*, of about 2 inches in length and placed it in a glass jar full of water, and 3 inches in diameter. I allowed the *Salpa* to fall from the surface of the cylinder to the bottom a number of times, and noted carefully the time which it took to traverse this distance, which was about 8 inches. I found that on the average it took 20 seconds to fall the 8 inches. This gives at the same rate, without allowance for acceleration, a distance of a fathom to be traversed in three minutes or 2,000 fathoms in four days four hours.

I allowed the *Salpa* to remain in the sea water in the cylinder for a long time. It was still not greatly decomposed after having remained in the same water for a month, whilst the ship was in the tropics; the nucleus was after this interval still undestroyed. The dead animal might have thus sunk to the bottom in the greatest depths almost six times over, without having become so much decomposed as to be unserviceable for food for deep sea animals."

Actually dead, but seemingly live specimens (because of their retarded deterioration) may thus be captured at any depth. A capture of a large number of salp specimens at greater depths still does not prove that they really lived there, as the sudden massive bloom (swarming), which is so typical for members of this group, is followed by an equally sudden disappearance, causing large numbers of salps to sink to lower strata more or less simultaneously. It seems safe to conclude that all salp species, including closely related ones, are essentially epipelagic, being largely confined to the euphotic zone.

4.4. Absence of other isolating mechanisms preventing exchange of genetic material

Intraspecific taxa may live completely sympatric and still be unable to cross-fertilize by having different reproductive seasons. Some well known examples exist in terrestrial animals. That this phenomenon is unlikely in salps may be illustrated by the distribution and abundance over several months of the year of two closely related taxa, *Thalia democratica* and *Thalia cicar*, in the CICAR-samples collected in the area around Curaçao, Aruba and Bonaire (Southern Caribbean). *Thalia cicar* is the dominant species, but the largest number of specimens of both species (cf. fig. 5) occurs in the same samples, viz. 88, 93, 97 and 98, indicating swarm-like conditions (probably caused by phytoplankton bloom at these stations) for both species simultaneously. Heron (1972) has studied the swarming of *Thalia democratica* off the Australian coasts. He discovered that the life span of a single generation during swarming conditions is as low as two days, the successive generations following each other at an extremely rapid pace. This must mean a tremendous reproductional activity. It is inconceivable that individuals of two populations swarming simultaneously and more or less at the same spot would not interbreed

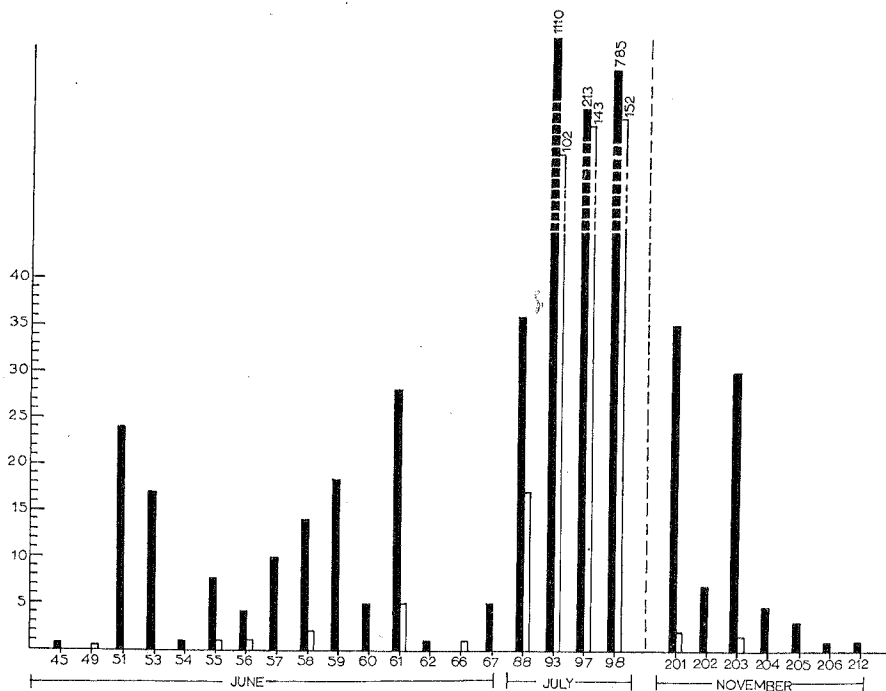


FIG. 5. Sympatric occurrence of *Thalia democratica* (white bars) and *Thalia cicar* (black bars) in the area around Curaçao, Aruba and Bonaire (southern Caribbean) CICAR 1970 Cruises 12-19). Horizontal axis: CICAR station numbers, vertical axis: no. of specimens.

were they conspecific. It seems almost certain that swarming periods of salp species are not caused by some intrinsic biological clock, but depend on environmental conditions (food, and to a lesser extent temperature and salinity). The seasonal occurrence of swarming is caused by the seasonal occurrence of favourable conditions. From the above given example it seems clear that *T. democratica* and *T. cicar*, even if under ideal circumstances for interbreeding, do not do so. Mutatis mutandis this is thought to be valid also for the other closely related salp taxa.

4.5. *The likelihood of genetic polymorphism*

Van der Spoel (1972), discussing heteropod speciation, mentions the possibility of genetic polymorphism as a solution to explain the occurrence of closely related sympatric forms in this group. There are only two sure ways of either proving or disproving the presence of one polymorphic species as opposed to the presence of several closely related species: that is by experimental breeding, or by observing the morphological variation in the offspring of one individual. If an individual produces offspring the individuals of which can be assigned on the basis of the morphological characters to two or more taxonomic units, then of course these are genetic morphs of one polymorphic species. In salps it is as yet impossible to completely disprove the occurrence of genetic polymorphism, because adequate breeding experiments have not been undertaken so far, and because the embryos, even in an advanced stage of development, generally do not show the characters distinguishing closely related taxa. An obvious way of checking this problem would seem to be the study of individuals of a chain of aggregate zooids, as they are attached to each other and originate from a single solitary zooid. However, as the aggregate chain is not a product of sexual reproduction, the individuals of the chain are genetically identical, and cannot be expected to show different morphs. Needless to remark, that different closely related taxa have never been found to occur in one and the same chain.

There is not much point in discussing the probability of genetic polymorphism in salps as long as any definite proof, one way or the other, is wanting.

4.6. *Closely related taxa in other zooplankton groups*

Finally it must be pointed out that the occurrence of apparently closely related sympatric taxa is not restricted to salps, but probably constitutes a fairly general phenomenon in many holoplanktonic groups. In Heteropoda (Mollusca) almost half the distant species has one or two closely related sympatric taxa next to it: *Atlanta inclinata* Souleyet, 1852 - *A. megalope* Richter, 1961, *A. helicinoides* Souleyet, 1852 - *A. fusca* Souleyet, 1852, *A. peroni* Lesueur, 1817 - *A. gaudichaudi* Souleyet, 1852 - *A. pacifica* Tokioka, 1955, *A. lesueuri* Souleyet, 1852 - *A. peresi* Frontier, 1966, *Carinaria lamarcki* Péron & Lesueur, 1810 - *C. challengeri* Bonnevie, 1920, *C. cristata* (Linnaeus, 1766) -

C. japonica Okutani, 1966, *C. cithara* Benson, 1835 - *C. procumbense* Tesch, 1949. Van der Spoel (1972) referred to these taxa as formae sensu van der Spoel (1971), but did not describe real intermediates (a primary demand for forma-status of the taxa), although discrimination between these taxa proves to be difficult due to the absence of clear taxonomic characters. Richter (1974), in the opinion of the present author rightly, considered all these taxa as full species. In Siphonophores (Coelenterata) several closely related sympatric pairs or groups of closely related species are known: *Diphyes dispar* Chamisso & Eyssenhardt, 1821 - *D. bojani* (Eschscholtz, 1829), *Abylopsis tetragona* (Otto, 1823) - *A. eschscholtzi* (Huxley, 1859), various *Lensia* Totton, 1932 species, various *Sulculeolaria* de Blainville, 1834 species (Totton, 1965; Alvariño, 1971; Pugh, 1974; own observations). In Euphausiids (Crustacea) Brinton's (1962) "central-equatorial groups of four species" (epipelagic) may be considered comparable, while in Pteropoda (Mollusca) the mesopelagic *Diacria trispinosa* (de Blainville, 1821) and *D. major* (Boas, 1866) may serve as good examples (Panhorst & van der Spoel, 1974). From these examples it is inferred that interference between environment and the holoplanktonic way of life in past and present ages is the cause of the phenomenon of closely related species.

4.7. Conclusions

Based on the above presented (partly circumstantial) evidence it is the firm conviction of the present author that the observed closely related sympatric forms in the Salpidae are not infraspecific taxa of polytypic species, nor genetic morphs of polymorphic species, but full species.

5. CLINAL VARIATION

In a previous paper (van Soest, 1972) it was reported that *Salpa fusiformis* in the Atlantic Ocean shows a neat latitudinal variation in the number of muscle fibres (and other biometric characters). In subsequent papers (van Soest, 1973a, 1974b, 1975) it was merely hinted that such a variation also exists in other species. It is now abundantly clear that latitudinal variation is a universal trend in all salp species with ranges extending far into temperate waters. The evidence for this will be presented below.

5.1. Latitudinal variation in *Salpa fusiformis* Cuvier, 1804

After the examination of more than one thousand individuals the original conclusion drawn in a previous paper (van Soest, 1972) for the Atlantic Ocean is applicable to all oceans. In fig. 6 the number of muscle fibres of aggregate specimens in samples from localities all over the three oceans is given. The figures represent the means of 3—25 specimens per sample, with some exceptions like the Bermuda area (56 specimens). A number of conclusions may be drawn from fig. 6. Firstly the number of muscle fibres in the tropical Atlantic is not different from that of tropical Indo-Pacific specimens. Secondly,

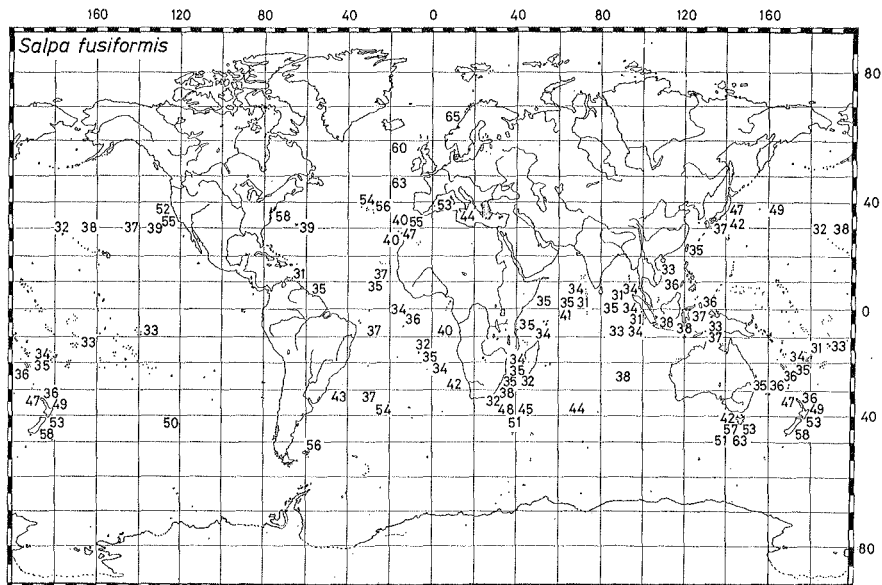


FIG. 6. Distribution of the mean numbers of muscle fibres of aggregate *Salpa fusiformis* samples over all three oceans.

the highest number of muscle fibres recorded from the temperate North Atlantic is clearly in excess of numbers reached in southern temperate waters, as well as in northern Pacific temperate waters, although the latter conclusion is based on thin evidence (only specimens from the California current and from East of Japan were available). Thirdly, in all oceans there is a transitional area between temperate and tropical waters, characterized by specimens with an intermediate number of muscle fibres. Some evidence seems to be present for the assumption that a further latitudinal variation — be it reduced — exists in the boreal North Atlantic: the northernmost localities yielded the highest means. Latitudinal variation within the tropical area seems to be absent, although a limited non-latitudinal variation is found. Figure 6 does not give information concerning a possible latitudinal shifting of the muscle fibre number along with the seasons; it is quite likely that this confuses to some extent the present picture.

Apart from biometric differences (cf. van Soest, 1972) no clearly defined differences have been found between temperate and tropical specimens. In general, tropical specimens are more delicately built due to their smaller size and narrower muscle bands.

5.2. Latitudinal variation in *Pegea confoederata* (Forskål, 1775)

Fig. 7 pictures the distribution of the number of muscle fibres of aggregate *Pegea confoederata* specimens over all three oceans. Again, the figures given represent the means of 3-25 specimens per sample. The differences between

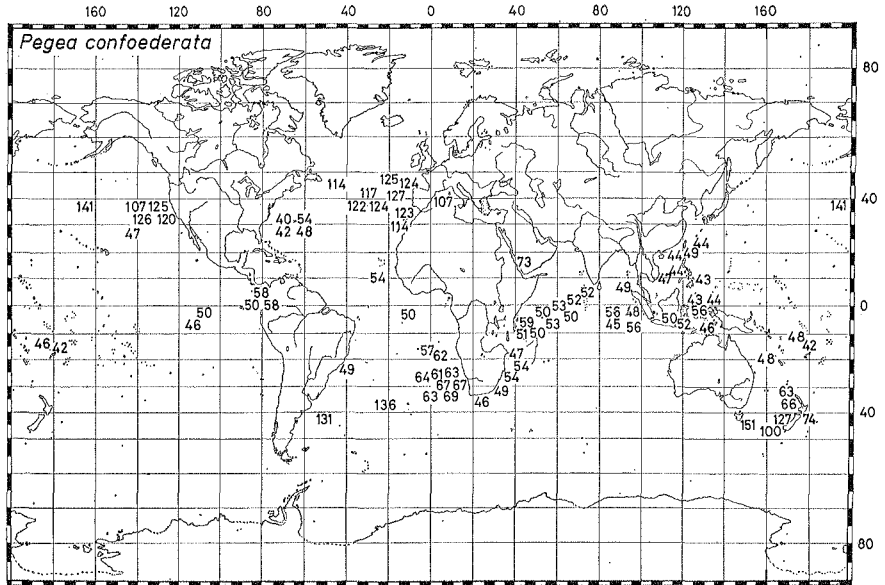


FIG. 7. Distribution of the mean numbers of muscle fibres of aggregate *Pegea confoederata* samples over all three oceans.

the number of muscle fibres in temperate and tropical specimens is spectacular. Temperate water specimens have numbers two or three times as high as tropical specimens. A relatively small number of samples shows intermediate values, indicating perhaps only narrow transitional zones for this species. Somewhat remarkable is the high number (73) found in a sample from the Red Sea, one of the warmest parts of the tropical zone.

Next to the difference in muscle fibre number a morphological difference between tropical and temperate specimens has been found. In temperate waters the third and the fourth body muscle (M III and M IV) of aggregate zooids approach each other but do not touch or fuse in the mid-dorsal region; in tropical specimens these are firmly fused. This morphological difference is found in all three oceans and it is clearly linked to the muscle fibre variation: Intermediate specimens from the transition zones have their M III - IV touching or barely fused. Similar but less conspicuous variation exists in the solitary zooids.

5.3. Latitudinal variation in other salp species

In table III all salp species showing latitudinal variation in their number of muscle fibres are listed. In some of them the variation has only been found in part of the range, of others not enough material was available to assess their variation in a latitudinal sense. From table III it can be concluded that almost all species distributed in tropical as well as temperate waters show the same

TABLE III. Salp species showing clinal variation in number of muscle fibres.

Species	Muscles counted	Mean number of muscle fibres (number of specimens counted)							Total	
		N. Atl.	Trop. Atl.	S. Atl.	S. Ind-Pac.	Trop. Ind-Pac.	N. Ind-Pac.	cold	warm	
<i>S. fusiformis</i>	sol.	M IV	27.8 (64)	21.2 (116)	27.1 (7)	26.3 (21)	19.8 (225)	26.4 (20)	27.2	20.3
	greg.	M I - VI	53.9 (146)	37.5 (98)	52.2 (9)	51.4 (46)	34.9 (227)	48.9 (48)	52.4	35.7
<i>P. confederata</i>	sol.	M I - IV	115.6 (3)	94.6 (15)	—	158.0 (1)	83.4 (50)	—	126.3	86.0
	greg.	M I - IV	120.0 (31)	58.6 (78)	135.5 (4)	105.1 (10)	51.5 (162)	122.1 (10)	118.8	53.8
<i>T. democratica</i>	sol.	M I - VI	63.3 (118)	52.3 (131)	58.1 (21)	64.0 (53)	42.7 (206)	59.1 (29)	62.5	49.5
<i>C. polae</i>	sol.	M I -VII	—	87.3 (4)	—	90.5 (2)	66.7 (16)	—	90.5	70.9
	greg.	M I - IV	23.5 (8)	24.0 (1)	—	31.0 (5)	23.4 (63)	22.9 (1)	25.9	23.5
<i>H. virgula</i>	sol.	M I -VII	281.6 (6)	217.8 (8)	—	—	221.0 (4)	229.0 (6)	264.1	217.8
	greg.	M I - IV	47.5 (9)	34.4 (3)	—	—	28.0 (3)	42.0 (6)	45.5	33.3
<i>I. punctata</i>	sol.	M I	238.0 (3)	153.2 (6)	—	—	105.7 (15)	226.5 (4)	231.4	117.6
	greg.	M I - II	97.0 (1)	74.8 (5)	—	—	63.8 (13)	—	97.0	66.8
<i>S. maxima</i>	sol.	M IV	74.7 (6)	50.2 (5)	—	74.0 (1)	51.0 (22)	—	74.6	50.9
	greg.	M I - VI	169.4 (19)	122.8 (10)	—	140.4 (5)	114.9 (19)	—	163.4	117.6
<i>T. vagina</i>	sol.	M IV- VI	157.0 (3)	134.0 (4)	—	—	122.8 (4)	—	157.0	127.1
	greg.	M I - V	272.3 (3)	223.8 (9)	268.0 (1)	—	174.0 (5)	—	271.3	206.1
<i>I. zonaria</i>	sol.	M III	112.0 (11)	100.4 (11)	116.6 (3)	153.5 (12)	64.0 (24)	91.4 (14)	117.6	75.4
	greg.	M I - V	123.7 (35)	90.3 (3)	100.7 (3)	165.3 (15)	61.7 (45)	92.3 (16)	122.0	76.3
Doubtful:										
<i>C. bakeri</i>	sol.	M I -VII	—	98.0 (2)	—	98.5 (2)	104.2 (5)	118.5 (24)	117.0	102.4
	greg.	M - IV	—	—	—	38.3 (10)	26.8 (6)	31.9 (10)	32.8	26.8
<i>S. aspera</i>	sol.	M IV	87.5 (2)	60.9 (61)	74.0 (2)	85.3 (2)	80.7 (37)	81.5 (4)	82.3	68.4
	greg.	M I - VI	159.8 (5)	115.5 (193)	168.5 (2)	150.3 (3)	132.3 (83)	178.1 (16)	170.7	120.5
<i>S. younti</i>	sol.	M IV	—	97.6 (8)	107.5 (2)	131.0 (4)	122.4 (27)	—	123.2	116.7
	greg.	M I - VI	—	201.0 (25)	231.3 (4)	262.3 (3)	208.9 (34)	190.0 (9)	213.7	205.5
<i>P. bicaudata</i>	sol.	M I - IV	128.0 (1)	125.5 (2)	132.7 (4)	—	111.0 (3)	—	131.8	116.8
	greg.	M I - IV	113.9 (7)	92.2 (10)	116.1 (6)	—	94.5 (19)	115.0 (1)	114.9	93.7
<i>C. pinnata</i>	sol.	M I -VII	169.0 (1)	—	—	—	—	—	169.0	—
	greg.	M I - IV	68.5 (13)	54.3 (3)	—	—	—	—	68.5	54.3

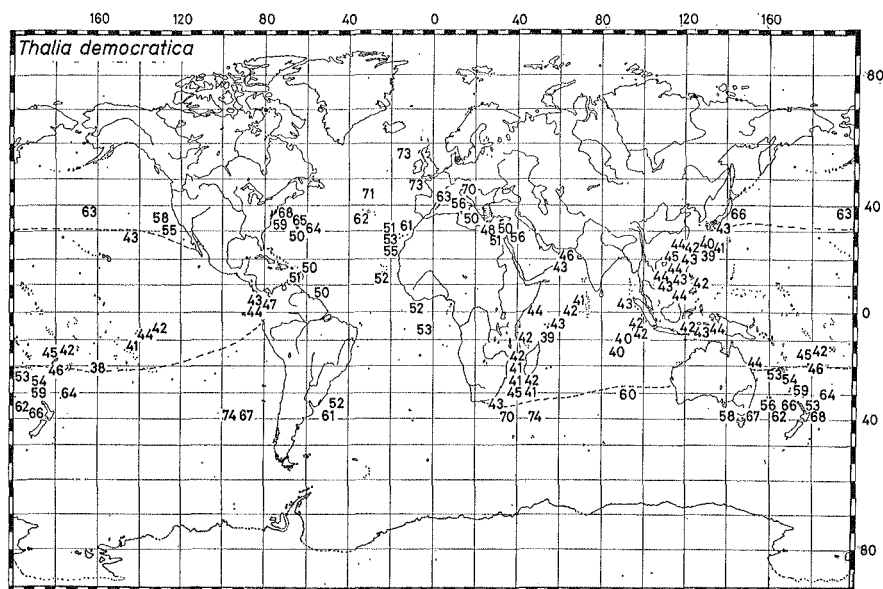


FIG. 8. Distribution of the mean numbers of muscle fibres of solitary *Thalia democratica* samples over all three oceans. Dotted line indicates the approximate limit of the distribution of *Thalia democratica* forma *indopacifica*.

latitudinal variation with a high number of muscle fibres in high latitudes and a low number in low latitudes.

Doubtful cases with regard to this variation are *Salpa aspera* (form with a high number of muscle fibres), *Salpa younti*, *Pegea bicaudata* (Quoy & Gaimard, 1833), *Cyclosalpa pinnata* (Forskål, 1775) and *C. bakeri* Ritter, 1905.

5.4. Latitudinal variation in *Thalia democratica* (Forskål, 1775)

A special section is devoted to *Thalia democratica* as this species shows not only latitudinal variation in the number of muscle fibres (in solitary specimens), but also a distinct morphological form in tropical Indo-Pacific waters. The latitudinal variation in the number of muscle fibres of the solitary zoid in all oceans is represented in fig. 8. It is immediately apparent that the values found in tropical Indo-Pacific waters are consistently lower than those found in the tropical Atlantic. Close comparison of specimens from both tropical regions has revealed a number of small morphological differences, which, however slight they were, clearly distinguish them. The northern temperate Atlantic, the tropical Atlantic, the southern temperate Atlantic, the temperate Indian Ocean, the southern temperate Pacific and the northern temperate Pacific waters all contain one morphological type with a limited variation. The tropical Indo-Pacific waters contain a slightly different type. A number of intermediate specimens has been found north of New Zealand.

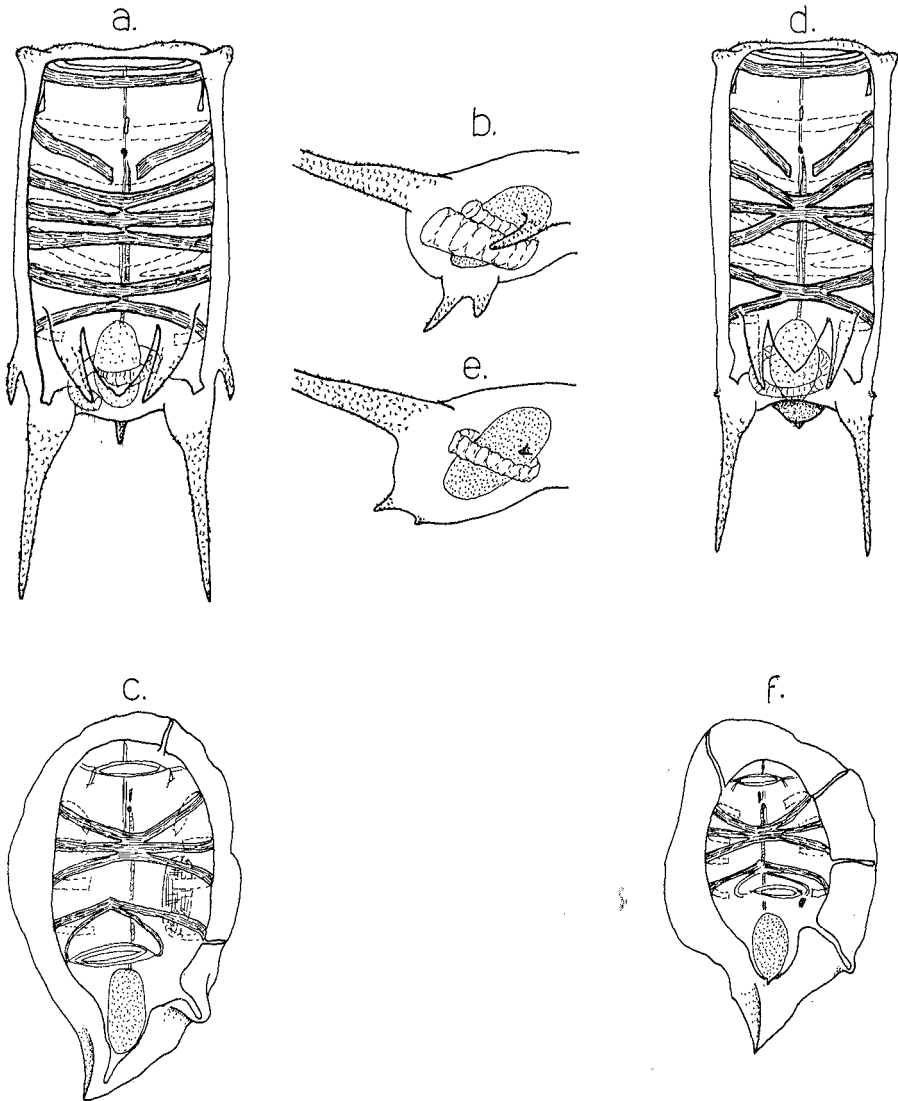


FIG. 9. a. *Thalia democratica* forma *democratica* sol. from the Bassin de Villefranche (W. Mediterranean), b. Lateral view of the posterior part of the same, c. Aggregate zooid of *T.d.* forma *democratica* from the same locality, d. Holotype of *T.d.* forma *indopacifica*, e. Lateral view of the posterior part of the same, f. Paratype (aggregate zooid) of *T.d.* forma *indopacifica*.

Without speculating about the status of these forms, it seems necessary to describe and name these forms, as they are clearly recognizable. Van der Spoel's (1971) forma - concept probably covers the present situation as the forms are allopatric and show intermediates. A discussion of the status of the latitudinal forms will be given below.

Thalia democratica (Forskål, 1775) forma ***democratica*** (Forskål, 1775)

Distinguishing characters (fig. 9a-c):

Solitary zooids: M II - M IV touching or barely fused in the mid-dorsal line. The number of muscle fibres of M I - M VI is 45 - 91 (n = 352). Lateral projections well developed, medio-ventral projections well developed.
Aggregate zooids: Test ending rather bluntly and bearing five rather blunt ridges posteriorly. Nucleus projection always present and mostly well developed.

Distribution (cf. also fig. 8):

This form is found all over the Atlantic Ocean, including the western and eastern parts of the Mediterranean; furthermore it occurs in subtropical and temperate parts of the Indo-Pacific.

Thalia democratica forma ***indopacifica*** nov.

Synonymy:

Thalia democratica local form, van Soest, 1973a: fig. 11a.

Type material:

Holotype: a solitary specimen from Siboga Expedition st. 144 (Salomakiee-Island, Indonesian Archipelago, 7/9-VIII-1899, bottom depth 45 m), incorporated in the Zoological Museum of Amsterdam under reg.no. TU. 1372.
Paratypes: 5 solitary specimens from the same locality as the holotype, incorporated under ZMA reg. no. 1373. Paratypes: 2 aggregate specimens from Siboga Expedition st. 136 (Ternate Island, Indonesian Archipelago, 29-VII/3-VIII-1899, bottom depth 23 m), incorporated under ZMA reg.no. 1374.

Distinguishing characters (fig. 9d-f):

Solitary zooids: M II - M IV firmly fused in the mid-dorsal line, although M II - M III are notably less firmly fused than M III - M IV. The number of muscle fibres of M I - M VI in the holotype is 42, in all investigated specimens it varied between 36 and 51 (n = 206). Lateral projections very weakly developed and barely visible. Medio-ventral projections weakly developed, the anterior one being merely a slight elevation.
Aggregate zooids: Test sharply ending and sharply ridged. Nucleus projection often absent, if present barely visible.

Distribution (cf. also fig. 8):

This form is confined to tropical Indo-Pacific waters, roughly between 25° - 30° N and 25° - 30° S. Specimens intermediate between the fo. *democratica* and the fo. *indopacifica* may be found in the subtropical transitional areas.

Non-latitudinal clinal variation in *Thalia democratica*:

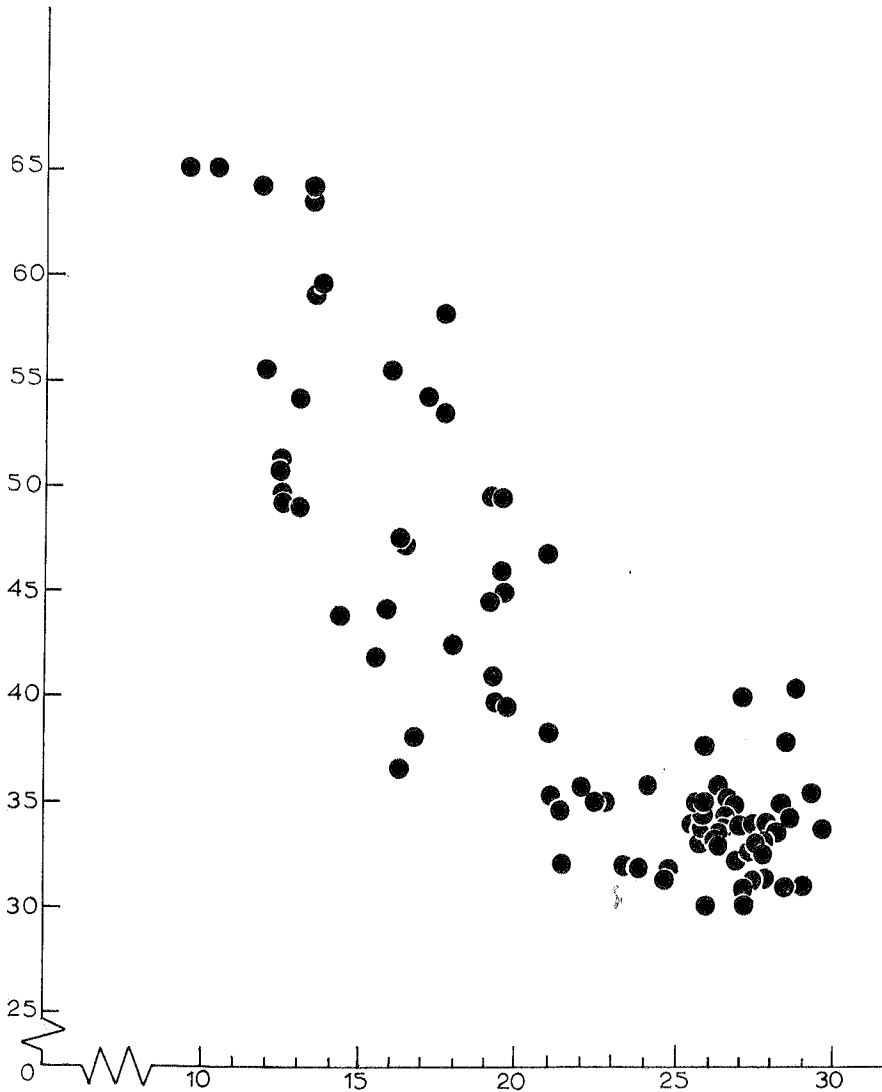


FIG. 10. Relation between sea surface temperature (horizontal axis) and the mean number of muscle fibres (vertical axis) of *Salpa fusiformis* greg.

Godeaux (1974) reported considerable differences in the number of muscle fibres of solitary specimens of *Thalia democratica* from the western and the eastern Mediterranean. A few specimens from the eastern Mediterranean, kindly donated by Prof. Godeaux, indeed showed a rather low number of muscle fibres (50 - 58), although not as low as given in table III of Godeaux's study on the salps of the eastern Mediterranean and the Red Sea (Godeaux, *loc. cit.*). The specimens clearly belonged to the f. *democratica*.

5.5. *Salpa thompsoni* Foxton, 1961, and *S. gerlachei* Foxton, 1961

It has been suggested in a previous paper (van Soest, 1974b) that *S. gerlachei* could be a clinal form of *S. thompsoni* as these taxa differ only biometrically and, more important, show intermediates (cf. Caldwell, 1966; Esnal, 1970). This view concurs with the fairly general trend in salp species with a wide distribution to form clinal variations.

5.6. Genetic forms (*formae sensu van der Spoel, 1971*) versus ecophenotypes

Is the latitudinal variation presented above the product of mere phenotypical adaptation to different environmental conditions (ecophenotypes) or are the tropical and temperate populations genetically different (*formae sensu van der Spoel, 1971*)? In favour of the former view (which is taken by Brinton (1962) in his description of the Pacific forms of the euphausiid *Stylocheiron affine* Hansen, 1910), is the apparent relation of the sea water temperature with the number of muscle fibres. An attempt has been made to picture this relationship for aggregate zooids of *Salpa fusiformis* (fig. 10) and *Pegea confoederata* (fig. 11). The sea water temperatures used are surface temperatures taken during sampling as these were the only ones available in the case of the Dana-samples. Many samples, however, have been captured at 50, 100 or more metres beneath the surface, at which depths temperatures are considerably lower than at the surface. Thus, some care should be exercised in interpreting figs. 10 and 11. Nevertheless, the relationship of temperature and number of muscle fibres is apparent, although it seems that in the temperature trajectory between 21° C and 15° C the increase in the number of muscle fibres is relatively steep, while it seems almost absent in the 30° C - 21° C trajectory. It may also be, that the number of muscle fibres is not directly related to the temperature, but to the density of the sea water, in which temperature mostly is the dominant factor. In *Pegea confoederata* specimens from the Red Sea the number of muscle fibres is higher than elsewhere in the tropical region, and this coincides with the higher salinity (causing higher density) of the Red Sea. *Salpa gerlachei* has a lower number of muscle fibres than *S. thompsoni*, although the temperatures at which both are living will not be very much different; the density of the water in the range of *S. gerlachei* is probably considerably lower, due to the low salinity of the sea bordering the ice edge, at least during the reproductive season. Other features presented above seem to support van der Spoel's (1971) forma-concept. In his opinion groups of populations of holoplanktonic species live separated because their respective habitats (the watermasses they live in) do not mix apart from border areas and they develop diversity as a result of different selective pressure of their environment. Eventually populations in the centre of each watermass or region would become genetically different from those in other centres, which would find its expression in more or less phenotypically differing individuals. In the boundary areas intermediate individuals would be found.

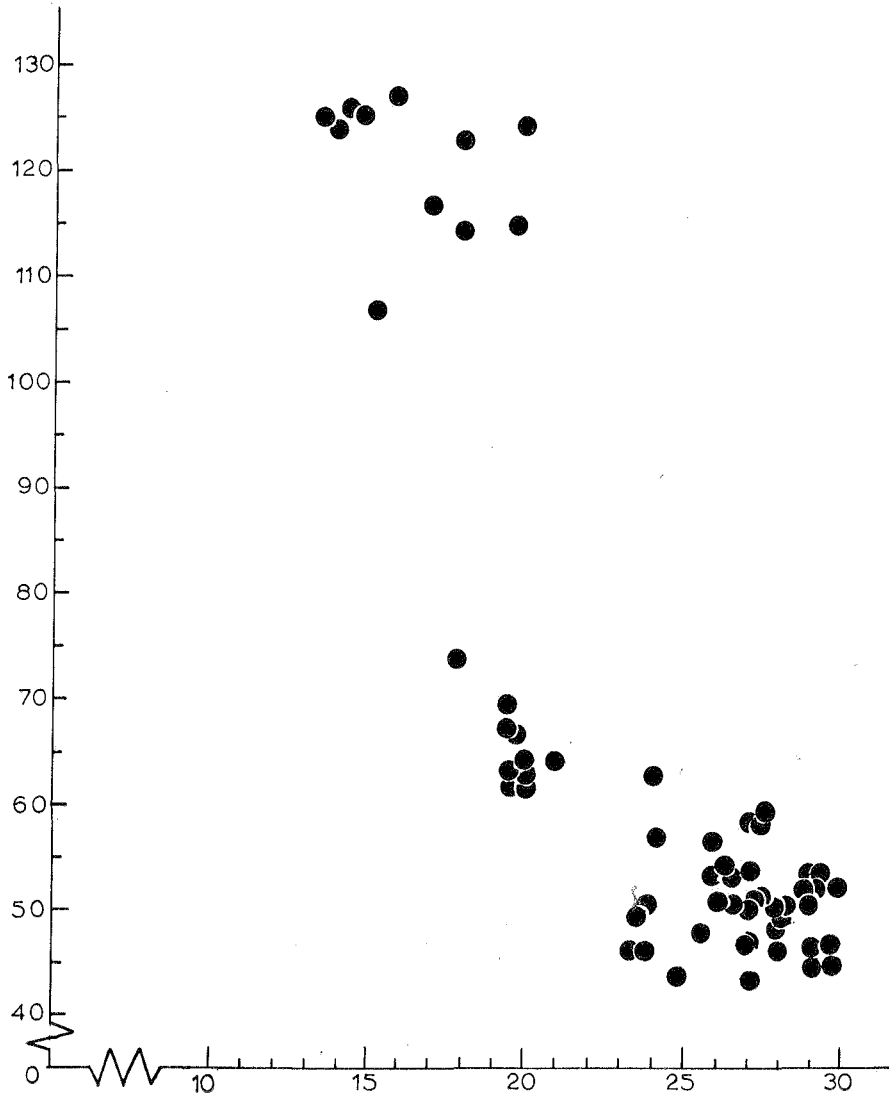


FIG. 11. Relation between sea surface temperature (horizontal axis) and the mean number of muscle fibres (vertical axis) of *Pegea confoederata* greg.

because mixing of the various watermasses then enables limited interbreeding. Although the term "forma" for the above described infraspecific taxa has been introduced by van der Spoel (1971) the phenomenon itself has already been described to some extent by Huxley (1942, 1949). Huxley's description of "stepped clines" (1949), or "dependent subspecies" (1942) covers the forma-concept more or less. A forma sensu van der Spoel (1971) may be considered as a special kind of subspecies, characterized by allopatric distri-

bution and zones of intergradation with other formae. Huxley (1949) sees no ground for introduction of separate names for each clinal form unless there are clear morphological and/or biometrical characters enabling an easy identification. In contrast to this van der Spoel (*loc. cit.*) points out the necessity to name every forma, whether characterized by morphological or only biometrical characters, as each is limited to a certain watermass and may be used as an indicator for it.

It is still undecided whether the latitudinal forms in salps represent genetically different populations or merely ecophenotypes. The relationship of temperature (or density) of the sea water and phenotype of the salp species may just as well be the product of genetical diversity, as the distribution of temperature coincides strongly with the zonation into distinct regions and watermasses of the oceans. As a matter of fact there can be no doubt that temperature (c.q. density) of the sea water is the major factor causing geographical north-south boundaries in the oceans and causing restriction of gene flow.

An indication of the forma-status of the described clinal variations may lie in the occurrence of certain salp species in subtropical and temperate waters without showing biometrical or morphological differences with tropical specimens of the same species. Examples in the North Atlantic Ocean are formed by *Traustedia multitentaculata* (Quoy & Gaimard, 1833), *Salpa aspera*, *Weelia cylindrica* and *Thalia orientalis* Tokioka, 1937. If the acquisition of a higher number of muscle fibres merely represents a phenotypical adaptation to different environmental conditions and moreover is a fairly uniform trend in species having an extensive distribution, then it cannot be understood why those particular four species do not show this adaptation. On the other hand, it could be explained by assuming that the occurrence into temperate waters of these species is only seasonal or temporal, their chief distribution being tropical.

To establish without doubt the genetical or non-genetical nature of the latitudinal forms in the Salpidae will only be possible by breeding experiments. Recently, attempts have been made by Heron (1972) to experimentally rear *Thalia democratica*. It is hoped that such attempts will continue and prove successful, in order to procure some answers to the problems raised in the present paper.

6. BIOGEOGRAPHICAL ZONATION OF THE SURFACE WATERS OF THE OCEANS BASED ON SALP DISTRIBUTION

Based on the above presented latitudinal variation and on an analysis of the various kinds of species distributions a horizontal zonation into faunal regions can be constructed. Table IV contains a classification of the Salpidae into groups of species with similar distributions. Four types of distributions seem to be apparent: a) a group of eurythermous species occurring to relatively high latitudes in all three oceans (60° N - 50° S), b) a group of less eurythermous species limited to between 40° - 45° N and 35° S, but equally occurring in all

TABLE IV. Groups of salp species having more or less the same geographical range.

	Med.	Atl.	Ind.	W.Pac.	E.Pac.
a. Widely distributed, eurythermous species:					
<i>Cyclosalpa polae</i>	×	×	×	×	×
<i>Cyclosalpa bakeri</i>	—	×	×	×	×
<i>Helicosalpa virgula</i>	×	×	×	×	×
<i>Ritteriella retracta</i>	—	×	×	×	×
<i>Brooksia rostrata</i>	×	×	×	×	×
<i>Ihlea punctata</i>	×	×	×	×	×
<i>Salpa fusiformis</i>	×	×	×	×	×
<i>Salpa maxima</i>	×	×	×	×	×
<i>Salpa aspera</i> (?)	—	×	×	×	×
<i>Thetys vagina</i>	—	×	×	×	×
<i>Iasis zonaria</i>	×	×	×	×	×
<i>Thalia democratica</i>	×	×	×	×	×
<i>Thalia orientalis</i>	×	×	×	×	×
<i>Pegea confoederata</i>	×	×	×	×	×
<i>Pegea bicaudata</i>	×	×	×	×	×
b. Less widely distributed, less eurythermous species:					
<i>Cyclosalpa affinis</i>	—	×	×	×	×
<i>Cyclosalpa danae</i>	—	×	×	×	×
<i>Cyclosalpa floridana</i>	—	×	×	×	×
<i>Cyclosalpa foxtoni</i>	—	×	×	×	×
<i>Brooksia berneri</i>	—	×	×	×	×
<i>Ritteriella amboinensis</i>	—	×	×	×	×
<i>Salpa younti</i>	—	×	×	×	×
<i>Weelia cylindrica</i>	—	×	×	×	×
<i>Thalia cicar</i>	—	×	×	×	×
<i>Traustedia multitentaculata</i>	—	×	×	×	×
c. Stenothermous warm water species:					
<i>Cyclosalpa sewelli</i>	—	—	×	×	×
<i>Cyclosalpa quadriluminis parallela</i>	—	—	×	×	×
<i>Cyclosalpa ihlei</i>	—	—	×	×	×*)
<i>Helicosalpa younti</i>	—	—	×	×	×*)
<i>Helicosalpa komaii</i>	—	—	×	×	×*)
<i>Ritteriella picteti</i>	—	—	×	×	×
<i>Metcalfina hexagona</i>	—	—	×	×	×
<i>Salpa tuberculata</i>	—	—	×	×	—
<i>Thalia rhomboides</i>	—	—	×	×	×
d. Species with a very restricted distribution:					
<i>Ihlea magalhanica</i> (subant.)	—	×	×	×	×
<i>Ihlea racovitzai</i> (antarct.)	—	×	×	×	×
<i>Salpa thompsoni</i> (subant.-antarct.)	—	×	×	×	×
<i>Salpa gerlachei</i> (high antarct.)	—	—	—	×	×
<i>Cyclosalpa pinnata</i>	×	×	—	—	—
<i>Thalia longicauda</i> (subant.)	—	×	×	—	—
<i>Thalia sibogae</i>	—	—	—	×	—
<i>Thalia rhinoceros</i>	—	—	—	×	—
<i>Cyclosalpa quadriluminis</i> f.					
<i>quadriluminis</i>	—	—	—	—	×
<i>Cyclosalpa strongyloenteron</i>	—	—	—	—	×

*) Pacific records from the Mid Pacific.

three oceans, c) a group of stenothermous warm water species limited to all tropical Indo-Pacific waters, and finally d) a heterogeneous group with a very restricted distribution either in subantarctic and antarctic waters or in parts of the tropical Pacific. This classification is still somewhat provisional as many species are not very well known. The northern Pacific Ocean north of 45° - 50° N is still unknown territory as far as salps are concerned. The above results in the zonation pictured in fig. 12. Eleven oceanic regions and subregions can be distinguished: I. Arctic region (characterized by absence of salps); II. North Temperate Atlantic region (70° N - 45° N in the eastern Atlantic, 52° - 40° N in the western part); III. Northern Transitional Atlantic region (45° - 20° N in the easternmost part and 40° - 35° N in the western part); IV. Tropical Atlantic region (20° N - 17° S in the eastern part, 35° N - 30° S in the western part); V. Southern Transitional region (southern Atlantic between 17° and 40° S on the eastern side and 30° - 37° S on the western side, southern Indian Ocean from 30° to 39° S and southern Pacific Ocean from 25° to 35° S on the western side and 5° to 25° on the eastern side); VI. Southern Temperate region (area between 37° and 45° S in the Atlantic, between 35° and $40^{\circ}/45^{\circ}$ S in the Indian Ocean, and between 25° and 40° S in the Pacific); VII. Circum-Subantarctic region (area between the subtropical and the antarctic convergence); VIII. Circum-Antarctic region (area between the antarctic convergence and the ice border); VIIIa. Pacific High Antarctic region (characterized by the occurrence of *Salpa gerlachei*); IX. Tropical Indian Ocean region (Indian Ocean north of 25° - 30° S); IXa. Tropical Western Pacific region (characterized by the presence of *Thalia rhinoceros* and the absence of *Cyclosalpa strongylopteron* and *C. quadriluminis* forma *quadriluminis* Berner, 1955); IXb. Tropical Eastern Pacific region (characterized by the absence of *Thalia rhinoceros* and *Cyclosalpa quadriluminis* forma *parallela* Kashkina, 1973, and the presence of *C.q.* forma *quadriluminis* and *C. strongylopteron*); X. Northern Transitional Pacific region (area between $25^{\circ}/30^{\circ}$ N and $35^{\circ}/40^{\circ}$ N presumably); XI. Northern Temperate Pacific region (area north of 40° N presumably).

Other subregions may perhaps be recognized: Subantarctic/Temperate Atlantic and Indian Ocean region (characterized by the distribution of *Thalia longicauda*), and the Indo-Malayan-Philippine area (characterized by the distribution of *Thalia sibogae* van Soest, 1973, of which a third record can be given here: Cheribon harbour, Indonesia, coll. P. Buitendijk, RMNHL. reg.no. 192).

The boundaries of all the recognized regions are of course not stable, but shift seasonally, as they are based on watermasses characterized each by their temperature and salinity. As important isotherms for the distribution of the various salp species may be considered the 10° C, 15° C and the 20° C annual mean surface isotherms. Whether or not the 25° C isotherm is of some importance is still undecided. Several species appear to be extremely stenothermous, never occurring in waters with temperatures below 25° C, for instance *Metcalfina hexagona* (Quoy & Gaimard, 1824), *Cyclosalpa sewelli*

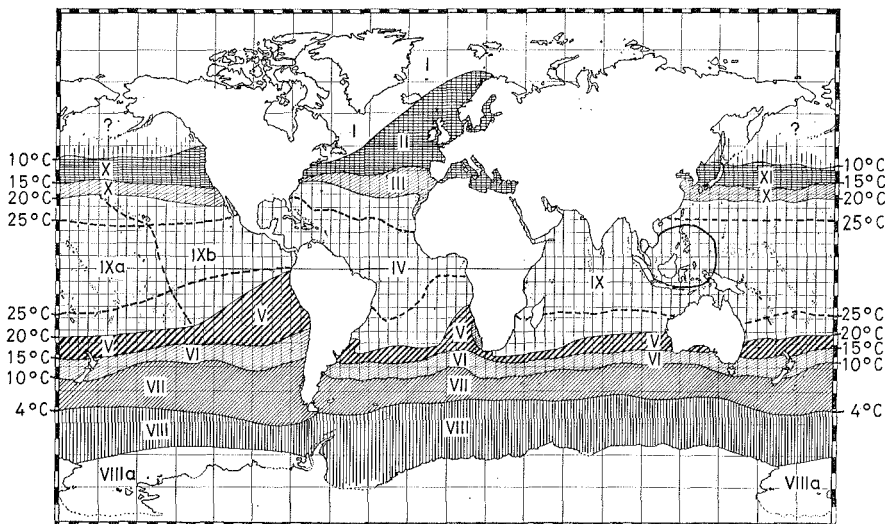


FIG. 12. Biogeographical subdivision of the world oceans based on salp distribution. For explanation see text.

Metcalf, 1927, *Salpa tuberculata* Metcalf, 1918, *Ritteriella picteti* (Apstein, 1904) and *Thalia rhinoceros*. In the Atlantic Ocean the 25° C isotherm is of no zoogeographic importance.

The zonation presented in fig. 12 is still a very generalized picture. It is as yet impossible to tell whether various species within the various regions are distributed randomly or according to certain patterns. It is not amazing to find that the zonation presented in fig. 12 largely conforms to similar biogeographic divisions of the oceans based on other holoplanktonic epipelagic groups, such as planktonic Foraminifera (cf. Bé & Tolderlund, 1971), polycistine radiolarians (Casey, 1971), planktonic copepods (Steuer, 1933), and epipelagic euphausiids (Brinton, 1962). Ekman (1953) and Briggs (1974) have given generalized biogeographic zonations of the pelagic habitat of the world oceans, differing not essentially from that based on salp distribution. Still, each group manifests its own zonations which differ in minor (subregional) points from those of other groups.

7. SPECIATION OF THE LOWER TAXA WITH A NOTE ON THE ORIGIN OF THE GENERA

The present state of our knowledge of the distribution and the relationships of the species of salps allows us to question the mode of speciation that has resulted in the species composition, particularly with regard to the closely related species described recently. As there is not a single fossil record known of salp-like animals, there is no way of guessing the age of the Salpidae as a whole. The group is considered as probably derived from other tunicate groups; it is obviously related to other pelagic tunicate groups as Pyrosomatids and Doliolids, together with which it is united to form the class Thaliacea. The

relationships within the Thaliacea and the origin of this class (probably derived from Ascidiacea-like ancestors) is still uncertain. Within the Salpidae the subfamily Cyclosalpininae, and within this the *Cyclosalpa pinnata*-group, contains probably the most primitive members. The genera *Pegea*, *Traustedtia* and *Thalia* are generally considered as the most specialized members (e.g. Metcalf, 1918). To these generalities little can be added; consignment of detailed categories of less primitive and more primitive genera falls outside the scope of this paper.

7.1 *Sympatric versus allopatric speciation*

The sympatric occurrence of groups of closely related species (for instance the *Thalia democratica*-group or the *Cyclosalpa pinnata*-group) always evokes the question whether this phenomenon is an indication of sympatric speciation having been at work. In the past decades several theories concerning sympatric speciation have been postulated, but they have never stood up to careful analysis (cf. Mayr, 1963). For oceanic zooplankton species (Pteropoda) such theories involving this have been launched as well (McGowan, 1963), but from van der Spoel's (1967) study of this group it appears that Mayr's (1963) arguments against this hypothetical process are valid against McGowan's ideas, too. Brinton (1962) used the information supplied by palaeontologists (e.g. Emiliani, 1955) to postulate theories involving geographic speciation in his attempts to explain the distribution of certain Pacific euphausiids. Emiliani (1955) analyzed core samples from the bottom of the Caribbean, the North Atlantic and the Eastern Pacific. He used Urey's (1947, after Emiliani, 1955) method of determining sea surface temperatures in past periods by measuring the O_{16}/O_{18} ratio in the $CaCO_3$ of pelagic foraminiferans. His results showed that in the Atlantic Ocean during the last million years several major fluctuations of the surface temperature must have taken place with an amplitude of about $6^\circ C$. In later papers Emiliani (1964, 1966) found an even greater fluctuation ($9^\circ C$). The Pacific Ocean was apparently less affected by these climatic deteriorations; the fluctuation of its temperature amounted according to Emiliani (1964) to $4^\circ - 6^\circ C$. The methods of Emiliani were very much criticized and this led McGowan (1971) to denounce Emiliani's results and Brinton's postulations. Colleagues of Emiliani (e.g. Olausson, 1965), however, have shown with improved techniques, that considerable decrease and increase of the sea surface temperature did occur in the Pleistocene period, although the lowest temperature during the whole of the period for the North Atlantic is estimated to be only about $3^\circ - 6^\circ C$ lower than the present temperature. Longinelli (1971) considered Emiliani's research to be one of the best pieces of work ever carried out in this field. Consequently, it seems that McGowan's arguments, that sympatric speciation in holoplanktonic closely related forms must have taken place because other mechanisms are lacking, are invalid. Geographic isolation in past, colder periods followed by reinvasion during subsequent warmer periods seems a likely explanation of the occurrence of sympatric close relatives. Sympatric speciation in salps is the more unlikely,

since there are no indications up till now, that the species of salps occupy different niches. The difference in size of some species means that they require different quantities of food, but it has never been shown that this also involves different kinds or sizes of food. The animals seem to lack selective feeding, if we disregard their ability to expel objects too large for coping with them. As far as is known preferences for certain depth strata are not present (cf. also the above section on vertical distribution). Theories on sympatric speciation almost invariably involve species occupying different niches (e.g. certain sibling species); it is inconceivable that such a theory could be devised successfully for salp speciation.

7.2. Geographic speciation of closely related taxa

If it is assumed that in several past periods the Atlantic Ocean sea surface temperatures have been about 6° C lower than at present, it is likely to expect that in quite a few presently living salp species (if they were existent at that time) gene flow between populations living in the Atlantic and those in the Indian and Pacific Oceans was blocked. In table V the lowest temperature limit is given at which each species (with the exception of the sub-antarctic and antarctic species) has been found to occur. From this list we learn that Atlantic populations of species having their lowest temperature limit at 8° C or higher would certainly have been cut off from Indo-Pacific populations, if we presume that the 8° C isotherm would have been at the position of the present day 14° C isotherm. It is furthermore quite clear that extremely stenothermous species (*Metcalfina hexagona*, *Cyclosalpa sewelli*, *Ritteriella picteti* and *Salpa tuberculata*) would be unable to continue living in the Atlantic, provided they did live there previously. Finally, such a de-

TABLE V. Lowest temperature limits at which species have been found to occur.

<i>Cyclosalpa pinnata</i>	12° C (?)	<i>Ritteriella picteti</i>	26° C
<i>Cyclosalpa polae</i>	12° C	<i>Metcalfina hexagona</i>	25° C
<i>Cyclosalpa sewelli</i>	25° C	<i>Ihlea punctata</i>	12° C
<i>Cyclosalpa quadriluminis</i>	23° C	<i>Weelia cylindrica</i>	17° C
<i>Cyclosalpa affinis</i>	15° C	<i>Salpa fusiformis</i>	6° C
<i>Cyclosalpa danae</i>	21° C	<i>Salpa maxima</i>	12° C
	(probably too high)	<i>Salpa tuberculata</i>	26° C
<i>Cyclosalpa floridana</i>	17° C	<i>Salpa aspera</i>	17° (N.Atl.), 5° C (S.Pacific)
<i>Cyclosalpa bakeri</i>	7° C	<i>Salpa younti</i>	19° C
<i>Cyclosalpa foxtoni</i>	14° C	<i>Iasis zonaria</i>	4° C
<i>Cyclosalpa ihlei</i>	22° C	<i>Thetys vagina</i>	12° C
<i>Cyclosalpa strongyloenteron</i>	?	<i>Pegea confoederata</i>	8° C
<i>Helicosalpa virgula</i>	12° C	<i>Pegea bicaudata</i>	13° C
<i>Helicosalpa younti</i>	25° C (?)	<i>Thalia democratica</i>	8° C
<i>Helicosalpa komaii</i>	25° C (?)	<i>Thalia orientalis</i>	12° C
<i>Brooksia rostrata</i>	15° C	<i>Thalia cicar</i>	15° C
<i>Brooksia bernerii</i>	20° C	<i>Thalia rhomboides</i>	21° C
	(probably too high)	<i>Thalia rhinoceros</i>	25° C
<i>Ritteriella amboinensis</i>	16° C	<i>Thalia sibogae</i>	25° C
<i>Ritteriella retracta</i>	12° C	<i>Traustedia multitentaculata</i>	16° C

crease of temperature would decidedly not prevent any gene flow between Atlantic and Indo-Pacific populations of a few eurythermous species, as *Salpa fusiformis*, *Thalia democratica*, *Pegea confoederata* and *Cyclosalpa bakeri*. Some of these do not have close relatives, and this would nicely coincide with the postulation of a temperature decrease of maximally 6° C; *Thalia democratica*, *Pegea confoederata* and *Cyclosalpa bakeri*, however, have sympatric close relatives, and to explain this a further decrease in the temperature should be postulated. Another possibility may lie in the assumption that oceanic circulations have changed in the past Pleistocene period.

For most cases of closely related species the above cited palaeoclimatological data provide adequate room for the assumption of allopatric speciation as the basic process responsible for the present species composition. We will briefly survey the categories of species within the Salpidae and their possible mode of speciation.

7.2.1. Pairs of closely related species both of which have a wide distribution

This category comprises *Pegea confoederata* - *Pegea bicaudata*, *Cyclosalpa bakeri* - *Cyclosalpa foxtoni* van Soest, 1974, *Cyclosalpa affinis* (Chamisso, 1819) - *Cyclosalpa danae* van Soest 1975, *Salpa aspera* - *Salpa younti*, *Brooksia rostrata* (Traustedt, 1893) - *Brooksia beneri* van Soest, 1975, and perhaps also *Thalia cicar* - *Thalia orientalis*, which seem to be more related to each other than to the remaining species of the *Thalia democratica*-group. All these pairs of species are postulated to have arisen as a result of Atlantic isolation of populations of a widely distributed, fairly eurythermous parent species, during one or more glaciation periods in the Pleistocene. Subsequent re-invasion of each other's range has taken place in warmer periods such as the present one.

7.2.2. Pairs of closely related species, one of which is confined to the Indo-Pacific area

This category comprises: *Ritteriella retracta* - *R. picteti*, *Salpa maxima* - *S. tuberculata*, *Helicosalpa virgula* (Vogt, 1854) - *H. younti*. The species confined to the Indo-Pacific area are stenothermous warm water species. During former colder periods Atlantic populations of the supposedly stenothermous parent species, isolated from the Indo-Pacific populations, had to adapt to lower temperatures (otherwise they would have perished), as the Atlantic Ocean has been shown to have been much colder during glaciation periods than the Indo-Pacific area. Indo-Pacific populations could retract into warm refugia without having to adapt their temperature tolerance. During climatic amelioration re-invasion of the Indo-Pacific by specifically different Atlantic populations is assumed to have taken place. A special case may perhaps be the *Cyclosalpa pinnata*-group of which both *C. sewelli* and *C. quadriluminis* are closely related to the widely distributed *C. polae*. This may be explained either

by assuming that speciation has taken place twice in different glaciation periods (a number of glaciations have been described in Pliocene and Pleistocene periods) or by assuming that the Pacific Ocean has been isolated to some extent from the Indian Ocean. The latter possibility will be discussed below.

Also referable to this category may prove to be the Indo-Pacific specimens of *Salpa aspera* and *Ritteriella retracta* with higher and lower numbers of muscle fibres (cf. van Soest, 1974b). If these prove to be different taxa then their origin might be explained in the same way as the above cited cases.

7.3. Geographic speciation of other taxa

7.3.1. Distant species:

It seems a fairly safe assumption that distant species or distant groups of species have diverged at an earlier date than the closely related species. It is thought that they originated according to the same processes as those thought to have given rise to the closely related species. As to the geological periods in which the speciation of distant species has taken place there seems to be no possibility of making an educated guess, except maybe the remark that it probably has taken place after the late Pliocene period (3.5 - 4.0 million years ago), as before this period the connection between North and South America linking the tropical Atlantic and Pacific has been open (Ekman, 1953; Briggs, 1974). Between this period and recent times a great number of climatic changes have taken place, some of which may have provided the environmental circumstances needed for most of the salp speciation.

7.3.2. Generic origin:

With the exception of the genus *Metcalfina* all salp genera are distributed over the warmer and temperate parts of all three oceans. *Metcalfina*, however, is restricted to Indo-Pacific waters; the limits of its distribution largely coincide with the 25° C isotherm. From our knowledge that the Pacific-Atlantic tropical sea way has been closed since the late Pliocene, it would seem to follow, that *Metcalfina* originated after its closure, because no *Metcalfina* species is living in the present day Atlantic. The extreme stenothermous behaviour of *Metcalfina*, however, could account for this fact; if the genus already existed in the Pliocene period and populations of it had been isolated in the tropical Atlantic after the closure, they almost certainly would have become extinct during later climatic deterioration with sea water temperatures in the tropical Atlantic as low as 22° - 20° C. It seems thus likely that all salp genera are of considerable age and speculations about their mode of speciation seem pointless considering the present state of our knowledge of the history of the oceanic basins and the absence of fossil records of salps.

7.3.3. Subantarctic and antarctic species:

The origin of the subantarctic species (*Thalia longicauda*, *Ihlea magalhanica*) and antarctic ones (*Salpa thompsoni/gerlachei*, *Ihlea racovitzai* van

Beneden & de Sélys Longchamp, 1913) presents a special problem. Apparently, their distribution is limited by hydrographical barriers such as the Subtropical and the Antarctic Convergences. It is rather tempting to assume that the present condition was initiated by the distribution of parent species exhibiting similar forms as the present day clinal forms in tropical and temperate waters. Such an assumption would require that strong barriers as the present Southern Ocean Convergences were absent or less strong in former periods; for this assumption there is no evidence available, although evidence for the opposite (long persistence of those strong barriers) is equally lacking. It seems quite conceivable, that oceanic circulation has been quite different during Pleistocene climatic deterioration periods.

The peculiar distribution of *Thalia longicauda* deserves a separate remark. Unlike *Ithlea magalhanica* which is distributed circumpolar, *T. longicauda* is up till now only found with certainty in the southern Atlantic and Indian Oceans (cf. also van Soest, 1973a). Recently studied samples from the southern Tasman Sea and south of eastern Australia (collected by the U.S.A.R.P. "El-tanin") did not contain a single specimen of this species, nor did the Dana-samples from east of New Zealand. It appears that a barrier south of Australia is present preventing its invasion of the Pacific. Apparently Australia also acts as a barrier for *Sagitta serratodentata* subsp. *atlantica* Thomson, 1947 (Chaetognatha), a subspecies, in contrast to *Thalia longicauda*, distributed in the southern Pacific and absent from the southern Indian and Atlantic Oceans (Pierrot-Bults, 1974).

7.3.4. Species confined to the Pacific Ocean:

This category comprises *Thalia sibogae*, *Thalia rhinoceros*, and *Cyclosalpa strongyleron*. The western Pacific Ocean has probably been partly isolated from the Indian Ocean during some of the Pleistocene Ice Ages by the emergence of the Java Sea - South China Sea shelf, due to lowering of the sea level (Umbgrove, 1929). Only a deep water channel east of Timor allowed exchange of faunal elements between Indian and Pacific Ocean, and it may well be possible that at least some species of salps have not passed through this channel. This could account for the origin of *Thalia rhinoceros* (found only in the western Pacific), although it remains a mystery why the species with the present open connections in the Indo-Malayan Archipelago did not penetrate recently into the Indian Ocean. *Thalia sibogae*, a species so far only found under neritic circumstances in the Indonesian and Philippine Archipelago, may have become isolated in submerged parts of the largely emerged shelf during the Pleistocene. Both *Cyclosalpa strongyleron* and *C. quadriluminis* forma *quadriluminis* are restricted as far as is known to the eastern Pacific, which is a distinct faunal region for sessile and neritic fauna, but is hard to accept as such for epipelagic, holoplanktonic, generally wide-spread salp species. That region is also separate from the rest of the Indo-Pacific as far as the distribution of species of other zooplankton groups, e.g. euphausiids (Brinton, 1962), is concerned. It seems that unknown ecological preferences

must play a rôle in restricting their distribution. It is thought that *Cyclosalpa strongylenteron* may well be a fairly original species (at least it is a "distant" one), although its relationship within the *Cyclosalpa bakeri*-group (cf. van Soest, 1974a) is still uncertain, due to the fact that only aggregate zooids and embryos have been described.

7.3.5. Development of clinal forms:

It is quite apparent that the latitudinal-clinal variation found in widely distributed species has arisen in postglacial times, during the climatic amelioration we are living in at present.

8. CONCLUDING REMARKS AND DISCUSSION

The present study has been an attempt to summarize the inventory of the lower taxa of the Salpidae, their status, distribution and zoogeography, and to arrive at a generalized view of the speciation in this group. The following conclusions are drawn:

1. Up till now 45 lower taxa have been described (including 4 formae sensu van der Spoel, 1971), divided over 13 genera. Another two possible taxa are found in Indo-Pacific waters (viz. forms of *Salpa aspera* and *Ritteriella retracta* with high and low number of muscle fibres).
2. Within the genera two kinds of species are recognized: distant species, which differ clearly and strongly, and closely related species which differ on minor, though equally clear points. The specific status of these closely related species is argued at length in this paper. Definite proof of this status is still wanting; future breeding experiments should be carried out to assemble conclusive evidence.
3. Closely related taxa include almost all taxa formerly described as subspecies. No evidence has been found for the occurrence of subspecies in the sense of Mayr (1963) in the Salpidae. Intraspecific taxa have been found, but these conform to the forma-concept of van der Spoel (l.c.), differing from Mayr's subspecies by the occurrence of intermediate characters in specimens from the boundary areas of the distribution of related formae.
4. Latitudinal variation in the number of muscle fibres has been found in all eurythermous species penetrating far into temperate waters. In high latitudes the number of fibres is high, in low latitudes it is low, in between intermediate numbers are found.
5. Although a general relation of the number of muscle fibres with sea surface temperatures has been found, strong arguments have been found for the assumption that the latitudinal-clinal variation is based on small genetic differences between populations living in colder and warmer waters. A special case is thought to be the Indo-Pacific tropical form of *Thalia democratica*, newly described in the present paper, which is distinguished by small morphological differences as well as differences in the number of muscle fibres from the typical form living in the tropical Atlantic and in temperate waters of

all oceans. Again breeding experiments under different temperature regimes should be undertaken to prove the genetic basis of these forms.

6. The distribution of the salp species is largely determined by sea surface temperatures.

7. On the basis of their distribution salp species can be divided into four groups: strongly eurythermous species, moderately eurythermous species, stenothermous warm water species, and species with a restricted distribution, either in subantarctic and/or antarctic waters or in parts of the Pacific Ocean.

8. Based on the distribution of salp species postulations have been made concerning the mode of speciation that has given rise to the present species diversity. The occurrence of sympatric speciation is thought to be unlikely, if not impossible. Palaeontological evidence, based on fossil foraminiferans, strongly points to the occurrence in the past 3.5 - 4.0 million years of several severe climatic deteriorations, accompanied by a considerable decrease of sea surface temperatures, followed by climatic ameliorations and increase of sea surface temperatures. The amplitude of temperature decrease and increase is estimated to be about 3° - 9° C for the Atlantic, the upper limit being roughly equal to the present temperatures. It is thought that decrease of sea surface temperatures during past glaciation periods has caused isolation of Atlantic populations of many salp species. This isolation apparently lasted long enough for specific differentiation. During climatic amelioration periods (such as the present one) reinvasion of Atlantic and Indo-Pacific Oceans by the former isolates is assumed to have given rise to the present sympatric occurrence of related species.

9. Weak hydrographical barriers, such as those found in the Transitional regions of all oceans seem to play a fairly important rôle in determining the distribution of many salp species and other zooplankton species and to cause infraspecific differentiation into clinal forms in other salp species and other zooplankton species. It is important to investigate these barriers to some further extent, using sophisticated sampling programs.

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