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VARIABILITY OF THE ORAL MUSCULATURE IN THE GENERA *SALPA* FORSKÅL, 1775 AND *WEELIA* YOUNT, 1954 (TUNICATA, THALIACEA).

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ABSTRACT

The aggregate zooids of *Salpa fusiformis* Cuvier, 1804, *S. maxima* Forskål, 1775, and the group of the species *S. aspera* Chamisso, 1819, *S. younti* Van Soest, 1973, *S. thompsoni* Foxton, 1961, and *S. gerlachei* Foxton, 1961, show a difference in the arrangement of the oral musculature. Differences in the solitary zooids are less clear. Differences have also been found in the total number of muscle fibres of the oral musculature in the aggregate zooids of the genera *Salpa* and *Weelia*. The aggregate and solitary zooids of the genus *Weelia* can be distinguished on their oral muscles from those of the genus *Salpa*. The aggregate zooids of *Salpa fusiformis* show clinal variation in the number of muscle fibres of the oral musculature.

INTRODUCTION

The holoplanktonic Salpidae use their body muscles to expel water from the pharyngeo-atrial chamber. The contraction of the body muscles throws the animal forward (Metcalf, 1918). The oral muscles close the oral aperture when the contraction sets in: these muscles, especially the oral sphincters, have to prevent the water from flowing out through the oral aperture. The lower and upper lip of the oral aperture act as valves, closing the oral aperture completely, as they have to resist the pressure of the ejecting water. In spite of this important function there are no clear literature data concerning the oral musculature. There are many contradictory statements in the literature as regards the arrangement of the separate muscles comprising this musculature. Streiff (1908) gives some drawings, viewed from the inside and outside of the body of several species of the Salpidae. Metcalf (1918) provides a few new figures besides those of Streiff. Most authors, however, just copied the figures of Streiff and Metcalf. Yount (1954) does not show oral and cloacal muscles in

most of his drawings, because these are small and difficult to indicate correctly in a drawing of the whole animal.

The arrangement of the muscles, especially the body muscles (cf. Van Soest, 1974), is one of the characters on which the species of the genus *Salpa* Forskål, 1775 are distinguished. Mostly, the body muscles can clearly be distinguished from the oral and the atrial musculature, but in some cases this distinction into three groups of muscles is arbitrary. The value of the arrangement of the oral muscles as a specific character can be assessed only by studying the variation of it within the species. This is the subject of the present study.

MATERIAL AND METHODS

The material studied consists of samples collected by various oceanic expeditions and a number of incidental samples. Localities, dates and the number of the solitary and aggregate zooids studied are enumerated in table I. In addition the localities of the samples studied are shown in figure 1. This study is based for the greater part on material incorporated in the collections of the Zoölogisch Museum, Amsterdam.

The formalin preserved specimens were first washed in destilled water during a few minutes (duration depending on the size of the specimens) after which the material was stained for a period of 20 minutes in a solution of 0.30 g alisarine-Red-S, 2.85 g natriumsulphate and 5 cm^3 acetate-acid 96% in 100 cm^3 aqua-dest. Next the material was washed in tap-water which resulted in red coloration of the musculature. It was then ready for study under a low power stereo-binocular microscope. Of a large number of aggregate zooids (exclusively ZMA-material) microscopic slides were made: the stained specimens were dehydrated in alcohol 96% during 5 to 10 minutes. The anterior part, containing the oral musculature, was cut off; with a small pair of scissors this fragment was cut at the ventral side along the endostyl and placed in glove oil for 5 minutes. Finally, the object was mounted in Rhenohistol.

In order to describe the variation of the oral musculature in the various species clearly, the separate muscles have been numbered in the same way in each species (for the numbers see figs. 2 and 3, and table II). The description and figures of the various species are based on observation of the musculature from the inside of the body in both aggregate and solitary zooids.

RESULTS

DESCRIPTION OF THE ARRANGEMENT OF THE ORAL MUSCULATURE

Genus *Salpa* Forskål, 1775

Salpa fusiformis Cuvier, 1804 (figs. 4-5)

Aggregate zooids: The oral aperture in the aggregate zooids of *Salpa* is situated dorsoanteriorly. There are two lips: the dorsal lip and the ventral one, the latter extending farther forward.

Muscle 1 bifurcates into muscles 4 and 5, just dorsad of muscle 2-3. Muscle 2-3 runs from dorso-posterior to ventroanterior, close to the endostyl. It crosses laterally underneath muscle 1. Muscles 4 and 5 run continuously from the left to the right side. Muscles 6 and 7, of which only muscle 7 runs uninterruptedly from the left to the right side, fuse into one near the junction of the muscles 4 and 5. They are attached to muscle 1 at the underside. Muscle 6 does not run from the left to the right side; it clearly terminates in the upper lip at the level of the dorsal horizontal muscle. Muscle 9, a branch of muscle 4, runs also from the left to the right side. The muscles 8 and 10 are branches of muscle 7, the former lies quite near to the place where muscles 6 and 7 fuse, the latter one further out along muscle 7. The muscles 8 and 10 run from the left to the right side, but muscle 8 becomes very thin and is interrupted in the middle of the lower lip. This was often very difficult to observe because numerous specimens were damaged at the lower and upper lip. A very important character by which the species of the genus *Salpa* can be distinguished is the way in which muscle 2-3 ends. In *Salpa fusiformis* it bifurcates, the thinner, longer branch runs more to the anterior end of the endostyl than the wider, shorter branch.

Solitary zooids (observed from the inside): The oral muscles of the solitary specimens are numbered in the same way as the aggregate specimens, but the numbers do not represent homologous muscles (see for the numbers table II). Muscle 1-9 passes under muscles 4 and 5 and runs uninterruptedly from

the left to the right side of the body. Ventral to muscle 1 and posterior to muscle 3, muscle 2 is found, which runs over a short distance from ventral-posterior to the angle of the crossing of muscles 1 and 3. It terminates underneath muscle 3, but is not connected with it. Muscles 4 and 5 cross muscle 1, muscle 5 runs uninterrupted from the left to the right side. Ventral to muscle 4 lies muscle 3; the muscles approach each other very closely, the gap between them lies underneath or just a bit ventrad of muscle 1. Ventral to the crossing of muscles 1 and 5 muscle 6 starts and it runs continuously from the left to the right side; muscle 6 is not attached to muscle 5. In the upper lip two other muscles are found: muscles 7 and 8. Muscle 7 is the longer one; it approaches muscle 5 very closely, but is not connected with it. Muscle 8 is the shorter one, lying more anteriorly in the upper lip; it is not attached to muscle 10, although it approaches muscle 10 very closely. Anterior to muscle 5, muscle 1 branches into muscles 9 and 10. These both run uninterruptedly from the left to the right side. It was sometimes very difficult to observe whether muscle 6 did or did not attach to the ventral part of muscle 5. Many specimens were badly damaged at the oral aperture, especially at the lower and the upper lip.

Salpa maxima Forskål, 1775 (figs. 6-7)

Aggregate zooids (fig. 6): Except for the ventro-terminal part of muscle 2-3 the arrangement of the oral muscles is the same as in *Salpa fusiformis* greg. In certain specimens muscle 8 runs continuously from the left to the right side of the oral aperture, but in some other specimens it is clearly interrupted in the middle of the lower lip, although both ends approach each other. The way muscle 2-3 terminates ventrally is different from *Salpa fusiformis*: the longer anterior branch of the bifurcate muscle has more muscle fibres than the shorter one. This situation is opposite as compared to *Salpa fusiformis*, in which the long branch has less muscle fibres than the short one.

Solitary zooids (fig. 7): Muscle 1, passing underneath the muscles 4 and 5, runs uninterruptedly from the left to the right side. Muscle 2 runs over a short distance from ventro-posterior to the angle of the crossing of muscles 1 and 4 and terminates in or near the gap between muscles 3 and 4. This gap between the muscles 3 and 4 is very broad; in two specimens they were still connected by a muscle fibre. At the ventral part of muscle 5, ventral to the crossing of muscles 5 and 1, muscle 6 branches off and runs continuously from the left to the right side. In the upper lip muscles 7 and 8 are found: muscle 7 is connected with muscle 5 just dorsal to the crossing of muscles 1 and 5; sometimes it runs continuously from the left to the right side, but in other specimens it is interrupted. Muscle 8 is a short muscle compared with muscle 7 and it runs anteriorly of muscle 7; muscle 8 is sometimes connected with muscle 10 but in other specimens there is no connection. Muscle 1 branches into muscles 9 and 10, anterior to the crossing of muscles 1 and 5. The muscles 9 and 10 both run from the left to the right side in the ventral lip.

Salpa tuberculata Metcalf, 1918

The scanty material available of this species (only a few aggregate zooids) could not be studied properly, due to its bad state of preservation. However, it could be established that muscle 2-3 in aggregate zooids bifurcates into a long and broad anterior branch and a short, fairly broad posterior branch, more or less like those in *S. maxima*.

Salpa aspera Chamisso, 1819 (fig. 8)

Aggregate zooids (fig. 8): The arrangement of the oral muscles is the same as in *Salpa fusiformis* greg. Only muscle 3 does not bifurcate at the ventral end, but it terminates broadly in comparison with *Salpa fusiformis*. In many specimens it was impossible to determine whether muscle 8 did run from the left to the right side or not, because the lower lip was damaged, or it was not clear whether the gaps in muscle 8 were natural or artificial. In those specimens where the lower lip was complete muscle 8 sometimes was indeed continuous, in other cases it was interrupted.

Solitary zooids: The oral muscles are arranged similarly to those of *Salpa fusiformis*, except for two differences: the muscles 6 and 7 are both attached to muscle 5, the former to the ventral part and the latter to the dorsal part of muscle 5, just anteriorly to the crossing of muscles 5 and 1. In one specimen muscle 8 is connected to muscle 10

with a single muscle fibre at the left side.

Salpa younti Van Soest, 1973

Aggregate zooids: The arrangement of the oral muscles is the same as in *Salpa aspera*. In *S. younti*, too, there are problems about muscle 8. Sometimes it was difficult to put on record whether the muscle did or did not run continuously from the left to the right side, because the specimens were somewhat damaged. In some slides muscle 8 was found running uninterruptedly from the left to the right side. In one specimen at the left side the ventral part of muscle 3 shows a small branch that runs a bit further than the main branch.

Solitary zooids: The arrangement of the oral muscles is the same as that of *Salpa maxima*. The muscles 7 and 6 are attached to muscle 5, the former just dorsal, the latter just ventral to the crossing of the muscles 5 and 1. The gap between muscles 3 and 4 is narrow. In two specimens muscle 8 is not attached to muscle 10 at both sides. In one specimen muscle 7 is bifurcated on the left side at the ventral part near muscle 5.

Salpa gerlachei Foxton, 1961

Aggregate zooids: The arrangement of the oral muscles is the same as that of *Salpa aspera* and *Salpa younti*.

Solitary zooids: The arrangement of the oral muscles is somewhat different from that of *Salpa aspera* and *Salpa younti*. Muscles 7 and 8 are not attached to muscles 5 and 10 and muscle 6 is not attached to muscle 5. In one specimen there was no gap between the muscles 3 and 4 at either side of the oral aperture.

Salpa thompsoni Foxton, 1961 (fig. 9)

Aggregate zooids: The arrangement of the oral muscles is the same as in *Salpa aspera*, *Salpa younti*, and *Salpa gerlachei*.

Solitary zooids (fig. 9): Muscles 3 and 4 show no gap near the crossing of muscles 1 and 4. The muscles 7, 8 and 6 are not attached to muscles 5, 10 and 5, so the arrangement of the oral muscles is quite the same as in *Salpa gerlachei*.

Genus *Weelia* Yount, 1954

Weelia cylindrica (Cuvier, 1804) (figs. 10-11)

Aggregate zooids (fig. 10): Muscle 2-3 runs from dorsoposterior to ventroanterior passing underneath muscle 1. Muscles 6 and 7 join underneath muscle 4 and they converge with muscle 5. Muscle 4 is attached with the dorsoterminal part to muscle 5. In the corner of the crossing of muscles 4 and 6 muscle 9 originates. Muscle 8 branches off from muscle 6. Muscle 10 is not connected to muscle 7. The muscles 4, 5, 7, 8, 9, and 10 all run continuously from the left to the right side. Muscles 4, 6, and 9 form the upper lip musculature and muscles 5, 7, 8, and 10 form the lower lip musculature of the oral aperture. Muscle 6 terminates farther in the upper lip at the level of the dorsal horizontal muscle. Muscle 3 is not bifurcated ventrally, but terminates broadly near the endostyl.

Solitary zooids (fig. 11): In all specimens studied there are differences with *Salpa* in the arrangement of the oral musculature. Muscle 1, which starts laterally close to the first body muscle, runs anteriorly, passing underneath muscles 4 and 5. There is no muscle 2. Muscles 3 and 4 show no gap. Muscle 6 is attached ventrally to muscle 1, just underneath the crossing of muscles 5 and 1. It runs continuously from the left to the right side. Muscles 7 and 8 fuse in the corner of the crossing of muscles 5 and 10: they are attached dorsally to muscle 1, just underneath the crossing of muscles 5 and 1. Muscle 7 runs continuously from the left to the right side, but muscle 8 is interrupted and short. The muscles 5, 7, and 8 form the upper lip. Muscle 5 is also continuous. Dorsad of the junction of muscles 6 and 1, but ventrad of the junction of muscles 7-8 and 1, muscles 9 and 10 branch off from muscle 1. Muscle 9 is continuous and forms with the muscles 10 and 6 the lower lip musculature of the oral aperture.

DIFFERENCES IN THE NUMBER OF MUSCLE FIBRES IN THE AGGREGATE ZOOIDS

In the present study the total number of muscle fibres of the oral muscles in the aggregate zooids has been counted (cf. table III). If one sample is considered representing a population it is allowed

to use the mean of the number of muscle fibres of a sample as a meristic of the population. The left and the right side have been considered separately, because the aggregate zooids are asymmetric.

The total number of the muscle fibres in the body muscles of salps is not correlated with age or growth of the individuals (Foxton, 1961), the individuals possessing a constant number of muscle fibres. So it is not necessary to allow for age or growth when comparing the number of fibres of the oral musculature in the genera *Salpa* and *Weelia* in the different parts of the Atlantic, Indian and Pacific Oceans.

From table III it is apparent that there are significant differences between the total number of muscle fibres of the aggregate zooids. For a correct assessment of these differences between the species one should compare counts made in the same locations, as some species show latitudinal variation in the number of muscle fibres.

LATITUDINAL VARIATION OF THE NUMBER OF MUSCLE FIBRES OF THE ORAL MUSCULATURE IN AGGREGATE ZOOIDS OF *SALPA FUSIFORMIS*

The total number of muscle fibres of the oral muscles has been counted (cf. table III). From higher to lower latitudes there is a decrease in the average total number of muscle fibres of the oral muscles in the Atlantic and Pacific Ocean. No material from the Indian Ocean was available. There was also no suitable material available from the more southern stations in the Atlantic Ocean and from stations between 30° N - 30° S in the Pacific Ocean.

CONCLUSIONS AND DISCUSSION

Comparing the results of this study with literature data the following differences are found: Streiff (1908, fig, 12) pictures the aggregate zooid of *Salpa maxima* correctly, except for the fact that muscle 10 is missing. In his drawing of the solitary form of *Salpa maxima* (fig. 9) the arrangement of muscles 1, 2 and 9 is not correct; muscle 10 is missing; and also there is no gap pictured between the muscles 3 and 4. Metcalf (1918, fig. 74) gives a drawing of the solitary form of *Salpa fusiformis*, in which there is no gap pictured between the muscles 3 and 4. The aggregate zooid of *Weelia cylindrica* (Metcalf, 1918: fig. 85) is shown without muscle 10, and muscle 9 does not branch off from muscle 4. Yount (1954, figs. 15a, 15b) illustrates the oral musculature of the aggregate zooids of *Salpa maxima* and *Salpa fusiformis*. The drawing of the oral musculature of *Salpa maxima* is correct except for muscle 2-3 which does not bifurcate at the ventro-anterior part. Muscle 10 is present in this drawing, but in the drawing of *Salpa fusiformis* muscle 10 is missing. Meurice (1974, fig. 9) shows the oral musculature of the aggregate *Salpa maxima* and *Salpa fusiformis*. In both drawings muscle 10 is missing. Sewell (1926, figs. 8 and 9) pictures the oral muscles of *Weelia cylindrica*, in two different forms of the solitary zooid. In both drawings muscle 10 is missing. Van Soest (1975, in press) does not show muscle 10 either in his drawings of the solitary zooid of *Weelia cylindrica*.

The aggregate zooids of the species of the genus *Salpa* tend to show small but constant differences. The distinction of the species *Salpa fusiformis*, *S. maxima*, and the group formed by the species *S. aspera*, *S. younti*, *S. thompsoni*, and *S. gerlachei* is based on the way muscle 2-3 ends at the ventral part near the endostyl (cf. table IV). Since these differences are constant within the species they are of distinctive value. Differences in the solitary zooids are less clear. Except for some small differences between the species of the genus *Salpa* (the muscles 3 and 4 show a clear gap in *S. maxima*, the muscles 6 and 7 are not attached to muscle 5 in *S. fusiformis*, *S. thompsoni* and *S. gerlachei*) there are no characters of distinctive value. Differences in the number of muscle fibres between the species are found, at least in aggregate zooids. The distinction between the genera *Salpa* and *Weelia* is well-marked in the characters of the arrangement of the oral muscles. The differences between *Weelia cylindrica* on the one hand and the species of *Salpa* on the other hand are greater than the differences between the various species of *Salpa* (cf. table IV). Within the species *Salpa fusiformis* a variability is found in the number of muscle fibres of the oral musculature of the aggregate zooids. This variation is similar to the variability in the number of fibres of the body muscles 1 to 6, which was studied by Van Soest (1972). By comparing the total number of muscle fibres of the body muscles

1 to 6 at different latitudes and latitudinal ranges Van Soest found a decrease in that total number of muscle fibres from higher to lower latitudes. In the present study the total number of muscle fibres of the oral musculature of the aggregate zooids of *Salpa fusiformis* has been compared for different parts of the oceans. A decrease in that number is found in the Atlantic and in the Pacific Ocean from higher to lower latitudes. This may be clinal variation, possibly related to density differences of the oceanic surface waters. For the greater part this density is determined by the water temperature; since the salinity in all the oceans, except for the eastern part of the Mediterranean, the Red Sea, the Arctic and Antarctic Ocean, does not vary much. Salinity is not taken into consideration in the present discussion on the adaptation to the density. If the temperature is lower the density is higher and the body muscles have to generate more power to transport the heavier water. When the body muscles develop more force, the oral muscles, especially the dorsal and the ventral lip musculature, have to resist a stronger water pressure. To develop more muscle fibres seems to be a logical adaptation to meet this pressure increase. The individuals of separate populations are characterized by a limited variation in the number of muscle fibres. Although a general correlation between muscle fibre number and sea surface temperature is observed (cf. fig. 12), other indications point against the assumption of a direct adaptation of the number of muscle fibres to meet changes of water temperatures. For example the differences in water temperature in the Western Mediterranean during the summer and winter seasons are considerable (24° C at 36°56' N 00°35' E, VIII-1970 and 11° C at 42° N 03° E, II-1932) but counts nevertheless give nearly the same results in the mean number of muscle fibres of the oral aperture musculature (viz. at the right side 50.88, at the left side 50.88; and at the right side 50.38 and the left side 50.63, respectively). Fig. 12 shows the correlation between water temperatures and the means and the ranges of the total number of muscle fibres of the oral musculature. The results (cf. table III) of left and right counts were in this case put together because there was no great difference between both sides of the oral aperture.

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Table I

STATION LIST

Station	Position		Date	No. of sol.	No. of greg.
Atlantic Ocean and Mediterranean Sea					
Cirrus st. M	65° N	03° E	3- X-1965		8
Cirrus st. I	59° 30' N	20° 00' W	3-VIII-1965		25
Tridens st. 3	44° 12' N	09° 02' W	30- V-1972		16
Tridens st. 4	43° 30' N	09° 44' W	30- V-1972		16
Villefranche-sur-Mer	42° 00' N	03° 00' E	II-1932		13
US-SI Med. 2-17B	41° 15' N	06° 51' E	1- IX-1970	1	
US-SI Med. 1-10M	37° 25' N	01° 07' E	22-VIII-1970	4	
US-SI Med. 1-5M	36° 56' N	00° 35' E	VIII-1970		17
Snellius Exped. India 2	33° 52' N	19° 20' W	12-VIII-1965		13
Acre st. 12-21M	32° 22' N	63° 43' W	2- IX-1971	1	
Acre st. 13-10M	32° 20' N	63° 33' W	25- II-1972		5
Acre st. 12-34C	32° 18' N	64° 03' W	7- IX-1971	1	
Acre st. 11-9N	32° 10' N	62° 49' W	14- I-1970	1	
Acre st. 13-24M	32° 08' N	63° 47' W	28- II-1972	3	17
Acre st. 13-25M	32° 08' N	63° 47' W	29- II-1972		3
Acre st. 14-8M	31° 58' N	63° 38' W	7- VI-1972	2	
Acre st. 13-28M	31° 54' N	64° 16' W	29- II-1972		4
Acre st. 13-27M	31° 51' N	64° 04' W	29- II-1972		1
Acre st. 10-10M	31° 51' N	64° 19' W	3- VI-1970		6
Acre st. 10-38N	31° 45' N	64° 48' W	6- VI-1970	1	3
Acre st. 13-21M	31° 41' N	63° 41' W	27- II-1972		3
Dana Exped. st. 4010^{IV}	27° 19' N	16° 41' W	19- III-1930	4	
Dana Exped. st. 4762	08° 13' S	02° 54' E	11- II-1933		4
Cicar 13	12° 07' N	68° 25' W	20- VI-1970		3
Cicar 12	08° 50' N	56° 00' W	16- III-1971	1	
Cicar 16/17 st. 008	04° 52' N	51° 41' W	26- IX-1970	2	
Willem Barendsz / st. 225	51° 58' S	20° 24' W	12- XII-1962		3
Willem Barendsz / st. 227	61° 59' S	38° 55' W	2- II-1963		5

continued overleaf

Table I, continued

Station	Position	Date	No. of sol.	No. of greg.
Indian Ocean (including the Red Sea)				
Red Sea (don. J. Godeaux)	26° 00' N 34° 05' E	III-1959		2
Willem Barendsz / st. 241	58° 09' S 27° 45' E	13- I-1960		7
Willem Barendsz / st. 352	64° 48' S 29° 58' E	9- II-1960		4
Willem Barendsz / st. 353	Antarctic waters	-		3
Dana Exped. st. 3932^{II}	11° 35' S 49° 35' E	20- XII-1929	3	3
Pacific Ocean (including the Indo-Malayan Archipelago)				
Dana Exped. st. 4779	30° 44' N 145° 55' E	19- IV-1933		15
Dana Exped. st. 4809	44° 33' N 168° 00' E	7- V-1934		3
Dana Exped. st. 4791	37° 42' N 147° 25' E	16- XII-1933		14
Dana Exped. st. 4892	32° 31' N 145° 21' E	7- IV-1934	3	11
Dana Exped. st. 3723^{V}	25° 30' N 125° 23' E	30- V-1929		2
Dana Exped. st. 3915^{II}	03° 14' N 73° 21' E	3- XII-1929		3
Dana Exped. st. 3561^{X}	04° 20' N 116° 45' W	24- IX-1928	3	2
Dana Exped. st. 3856^{IV}	04° 45' S 98° 28' E	12- X-1929		4
Dana Exped. st. 3627^{VI}	30° 08' S 176° 50' W	14- XII-1928	2	
Dana Exped. st. 3654	33° 28' S 161° 45' E	27- I-1929		9
Dana Exped. st. 3640^{VI}	41° 47' S 176° 55' E	7- I-1929		3
Dana Exped. st. 3640^{VIII}	41° 47' S 176° 55' E	7- I-1929		25
Dana Exped. st. 3642	46° 43' S 176° 08' E	9- I-1929	2	
Siboga Exped. st. 128	04° 27' N 125° 25' E	22- VII-1899		1
Siboga Exped. st. 148	00° 17' S 129° 14' E	10-VIII-1899		5
Siboga Exped. st. 36	07° 38' N 117° 31' E	29- III-1899		6
Leba-leba baai (Lomblen)	08° 50' S 123° 50' E	8- II-1909	1	
US Eltanin 38 st. 2241	40° 02' S 152° 07' E	10- V-1969	2	
US Eltanin 28 st. 1942	43° 15' S 148° 14' E	12- III-1967		12
Discovery Exped. st. 1257 (don. P. Foxton)	67° 52' S 129° 27' W	11- I-1934	2	3

Table II

EXPLANATION OF THE NUMERALS GIVEN TO THE VARIOUS ORAL MUSCLES

Aggregate zooids:

1	:	oral retractor
2-3	:	intermediate muscles
4	:	third dorsal sphincter
5	:	fourth ventral sphincter
6	:	first dorsal sphincter
7	:	third ventral sphincter
8	:	first ventral sphincter
9	:	second dorsal sphincter
10	:	second ventral sphincter

Solitary zooids:

1	:	oral retractor
2	:	? second oral retractor
3-4	:	complex of the intermediate muscles
5	:	third dorsal sphincter
6	:	third ventral sphincter
7	:	second dorsal sphincter
8	:	first dorsal sphincter
9	:	first ventral sphincter
10	:	second ventral sphincter

Table III

RANGES AND MEANS OF THE NUMBER OF MUSCLE FIBRES OF THE ORAL MUSCULATURE IN THE AGGREGATE ZOOIDS OF THE VARIOUS SPECIES FROM DIFFERENT LOCATIONS

Position	Mean of right side	Range	Mean of left side	Range	No. of spec.	Mean and range of both sides		Temp.
Salpa fusiformis Cuvier, 1804								
65° N 03° E	57.00	53-61	55.63	51-61	8	56.31	51-61	9.5° C
59°30' N 20°00' W	53.36	51-58	53.36	46-60	25	53.36	46-60	14 ° C
44°12' N 09°02' W	53.80	47-65	53.20	48-61	16	53.50	47-65	13.8° C
43°30' N 09°44' W	54.25	47-60	53.56	49-57	16	53.65	47-60	13.9° C
33°52' N 19°20' W	43.92	40-48	44.57	42-48	13	44.25	40-48	19 ° C
32°08' N 63°47' W	45.41	42-50	45.12	42-52	17	45.27	42-52	19.5° C
32°08' N 63°47' W	38.66	38-40	38.66	38-40	3	38.66	38-40	19.5° C
31°54' N 64°16' W	45.61	42-48	42.75	41-44	4	44.18	41-48	19.5° C
31°51' N 64°04' W	44.00	- - -	41.00	- - -	1	42.50	- - -	19.5° C
42°00' N 03°00' E	50.38	47-55	50.63	46-57	9	50.55	46-57	11 ° C
36°56' N 00°35' E	50.88	45-61	50.88	46-55	17	50.88	45-61	24 ° C
37°42' N 147°25' E	48.86	42-54	48.93	45-55	14	48.90	42-55	17.2° C
32°31' N 145°21' E	44.30	41-49	45.45	42-48	11	44.88	41-49	15.6° C
30°44' N 145°55' E	44.31	40-49	44.25	40-49	15	44.28	40-49	18.2° C
33°28' S 161°45' E	43.44	41-45	42.75	41-44	9	43.10	41-45	23 ° C
41°47' S 176°55' E	50.50	49-52	48.66	46-53	3	50.80	45-60	17.7° C
41°47' S 176°55' E	52.40	47-60	51.63	45-57	25			
43°15' S 148°14' E	48.42	46-52	48.58	46-55	12	48.50	46-55	13.9° C
04°27' S 125°25' E	39.00	- - -	38.00	- - -	1	38.50	- - -	26.5° C
00°17' S 129°14' E	43.50	40-45	43.60	36-48	5	43.55	36-48	27 ° C
07°38' S 117°31' E	41.33	40-43	40.67	37-44	6	41.50	37-44	26.5° C
Salpa maxima Forskål, 1775								
42°00' N 03°00' E	217.50	220-233	219.00	210-228	2	- - -	- - -	- - -
12°07' N 68°25' W	171.66	159-183	170.00	167-179	3	- - -	- - -	- - -
Salpa aspera Chamisso, 1819								
08°21' S 02°54' E	103.33	99-106	109.66	109-119	3	- - -	- - -	- - -
Salpa younti van Soest, 1973								
30°20' N 63°33' W	235.00	217-253	234.00	- - -	2	- - -	- - -	- - -
03°14' N 73°21' E	241.00	227-239	248.00	222-266	3	- - -	- - -	- - -
04°20' S 116°46' W	260.00	256-264	246.50	245-248	2	- - -	- - -	- - -
Salpa thompsoni Foxton, 1961								
51°58' S 20°24' W	178.33	173-181	175.66	162-198	3	- - -	- - -	- - -
Weelia cylindrica (Cuvier, 1804)								
26°00' N 34°05' E	94.50	91-98	95.00	92-98	2	- - -	- - -	- - -
05°52' S 106°36' E	82.50	82-83	84.00	83-84	2	- - -	- - -	- - -

Table IV

SUMMARY OF THE OBSERVED DIFFERENCES IN THE ARRANGEMENT OF THE ORAL MUSCLES IN AGGREGATE AND SOLITARY ZOOIDS OF THE GENERA *SALPA* AND *WEELIA*

Species	Aggregate zooids	Solitary zooids
Salpa fusiformis	M 2-3 bifurcating at ventral part ; anterior branch long and thin, posterior branch short and broad. M 4 fusing smoothly into M 5. M 8 branching off M 7.	M 2 present. Narrow gap between M 3 and M 4. M 6 and M 7 not attached to M 5.
Salpa maxima	M 2-3 bifurcating at ventral part; anterior branch long and broad, posterior branch short and narrow. Furthermore as in *S. fusiformis*.	M 2 present. Wide gap between M 3 and M 4. M 6 and M 7 attached to M 5, viz. to its dorsal and ventral part.
Salpa aspera	M 2-3 terminating broadly. Furthermore as in *S. fusiformis*.	M 2 present. Narrow gap between M 3 and M 4. M 6 and M 7 attached to M 5, viz. to its ventral and dorsal part.
Salpa younti	M 2-3 terminating broadly. Furthermore as in *S. fusiformis*.	M 2 present. Narrow gap between M 3 and M 4. M 6 and M 7 attached to M 5, viz. to its ventral and dorsal part.
Salpa thompsoni	M 2-3 terminating broadly. Furthermore as in *S. fusiformis*.	M 2 present. No gap between M 3 and M 4. M 6 and M 7 not attached to M 5.
Salpa gerlachei	M 2-3 terminating broadly. Furthermore as in *S. fusiformis*.	M 2 present. Narrow gap between M 3 and M 4. M 6 and M 7 not attached to M 5.
Weelia cylindrica	M 2-3 terminating broadly. M 4 terminating in junction of M 5 and M 7. M 8 branching off M 6.	M 2 missing. No gap between M 3 and M 4. M 6 and M 7-8 attached to M 1.

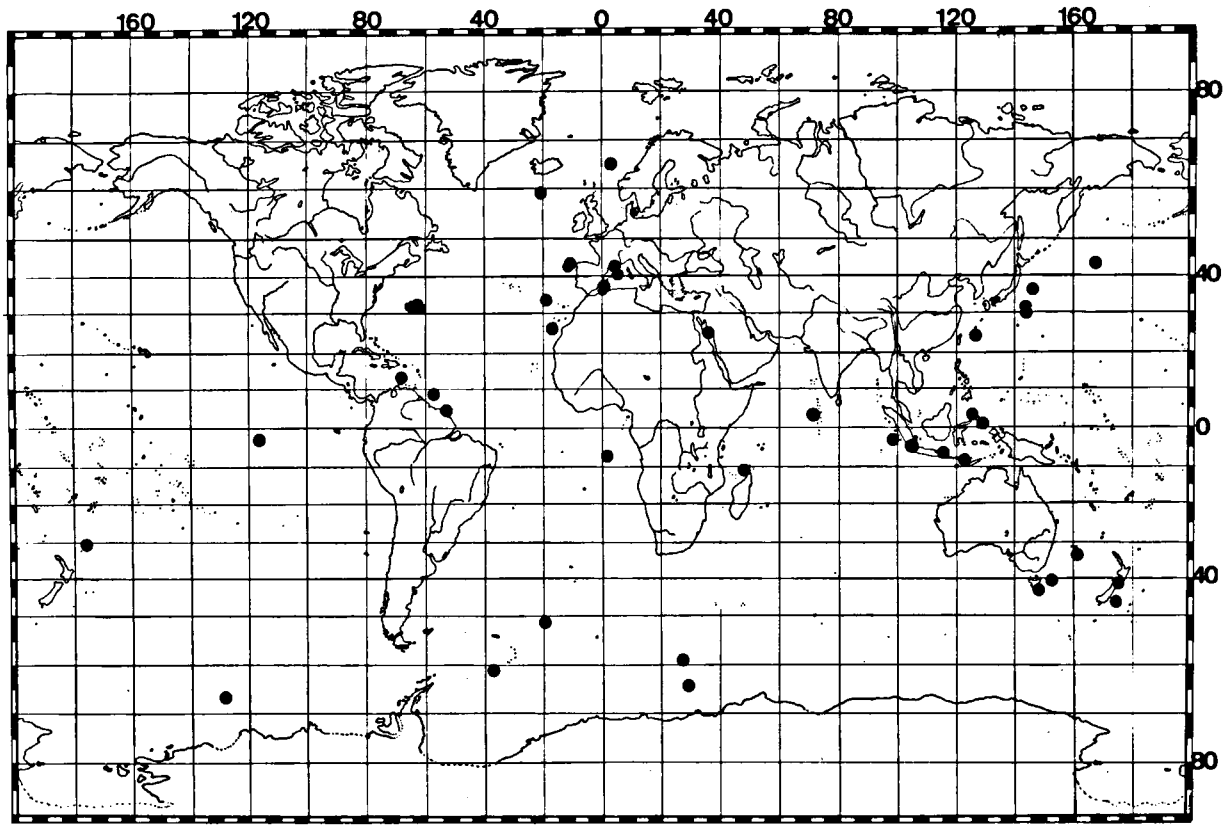

Fig. 1 Locations of the samples studied.

FIG. 2

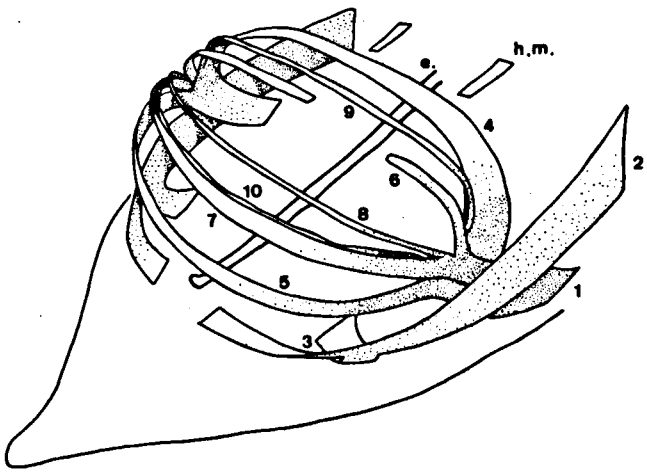

FIG. 3

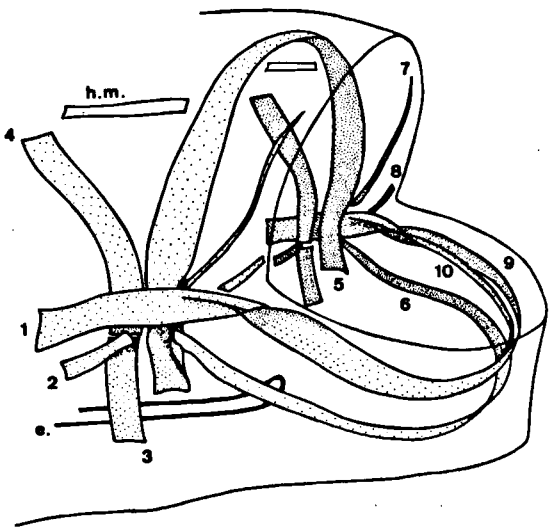

FIG. 4

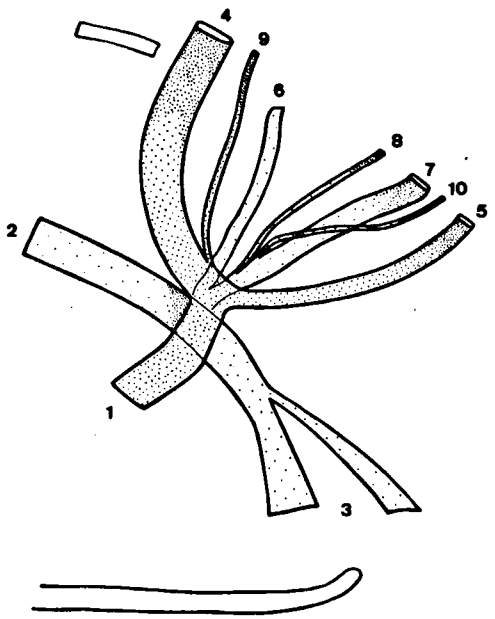

FIG. 5

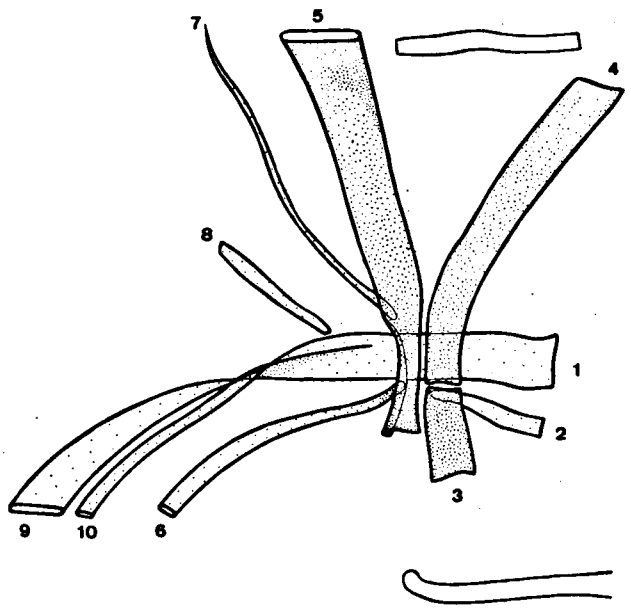

Fig. 2 Diagrammatic representation of the anterior part of an aggregate zooid of *Salpa* sp., showing the spatial arrangement of the oral muscles (h.m. = horizontal muscle, e. = endostyl).

Fig. 3 Diagrammatic representation of the anterior part of a solitary zooid of *Salpa* sp., showing the spatial arrangement of the oral muscles.

Fig. 4 Diagrammatic, two-dimensional representation of the oral musculature on the left side of the aggregate zooid of *Salpa fusiformis*, seen from the inside of the body.

Fig. 5 The oral musculature of the solitary zooid of *Salpa fusiformis* (right side, seen from the inside of the body).

FIG.6

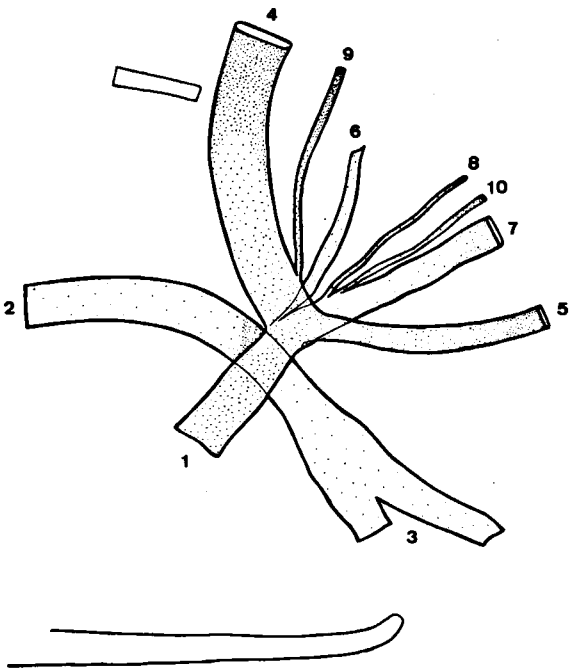

FIG.7

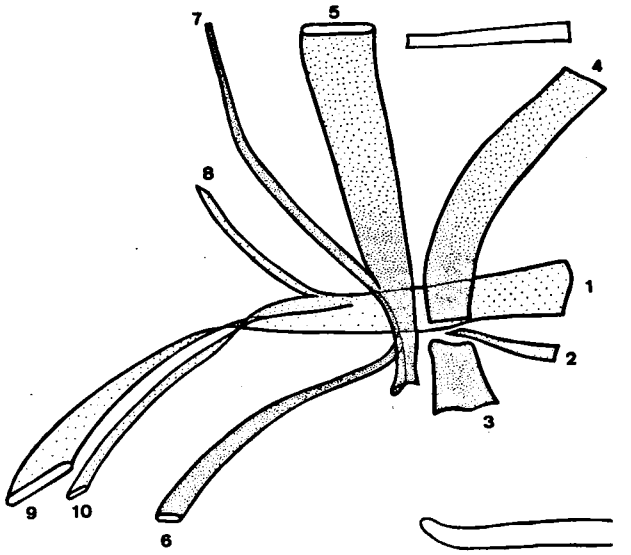

FIG.8

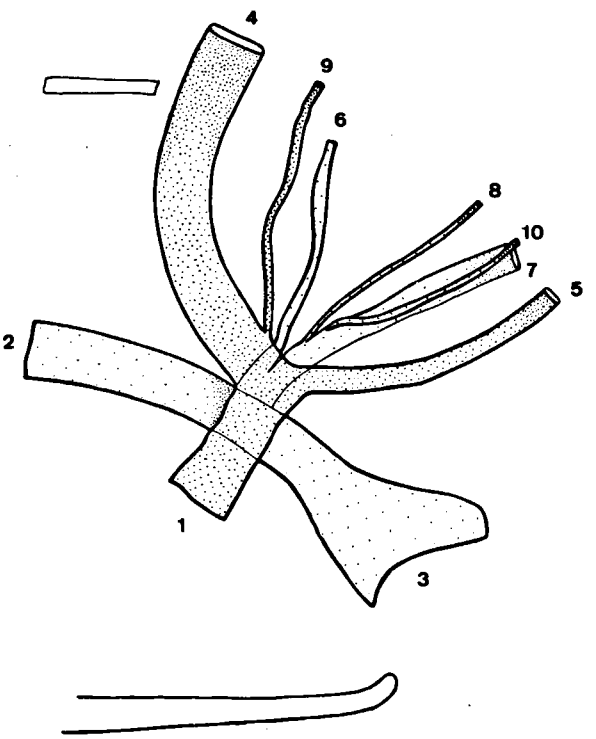

FIG.9

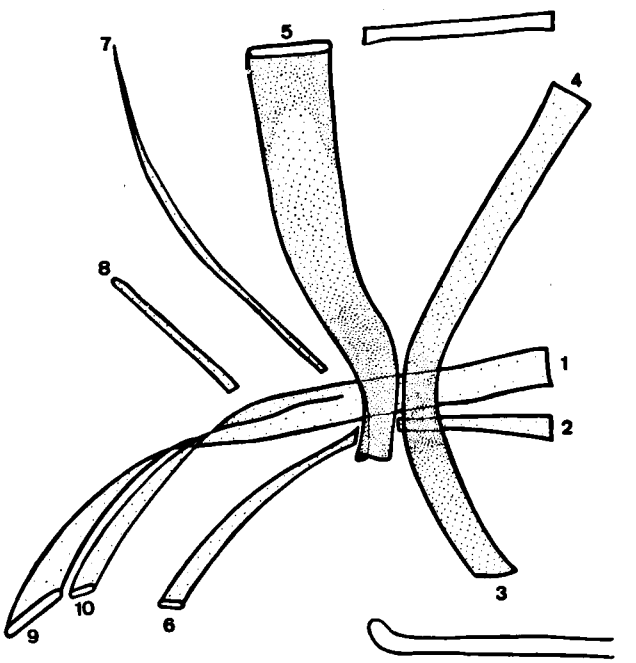

Fig. 6 The oral musculature of the aggregate zooid of *Salpa maxima*.

Fig. 7 The oral musculature of the solitary zooid of *Salpa maxima*.

Fig. 8 The oral musculature of the aggregate zooid of *Salpa aspera*.

Fig. 9 The oral musculature of the solitary zooid of *Salpa thompsoni*.

FIG.10

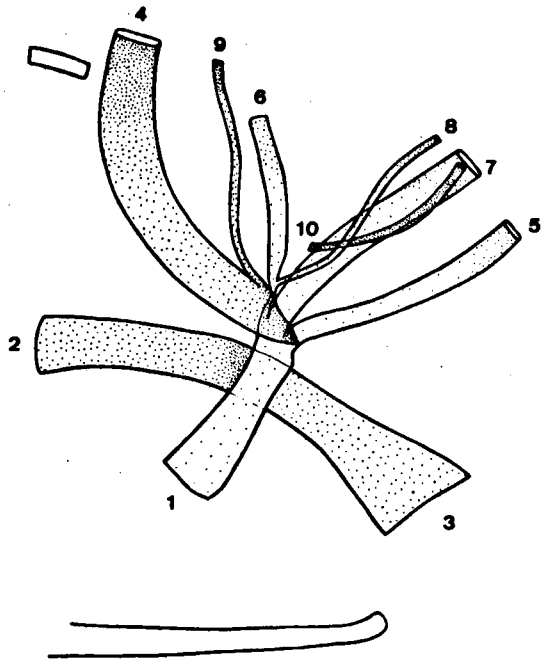

FIG.11

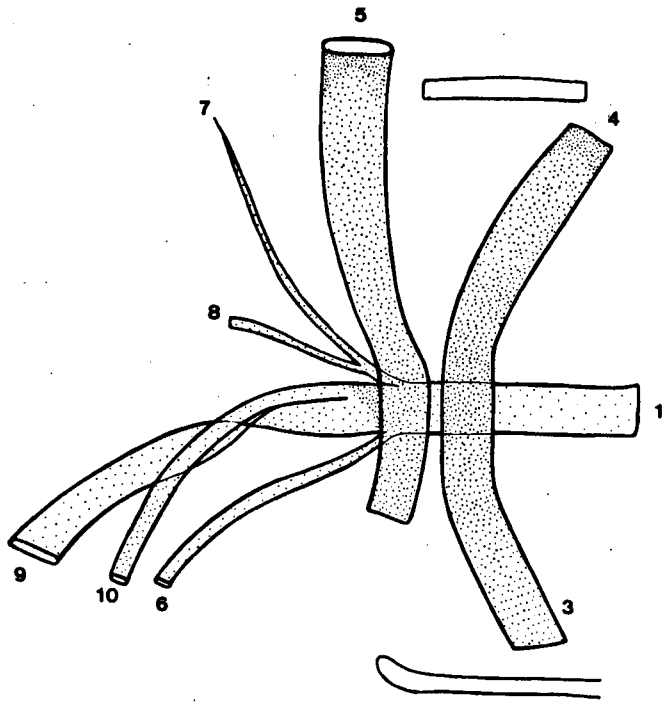

Fig. 10 The oral musculature of the aggregate zooid of *Weelia cylindrica*.

Fig. 11 The oral musculature of the solitary zooid of *Weelia cylindrica*.

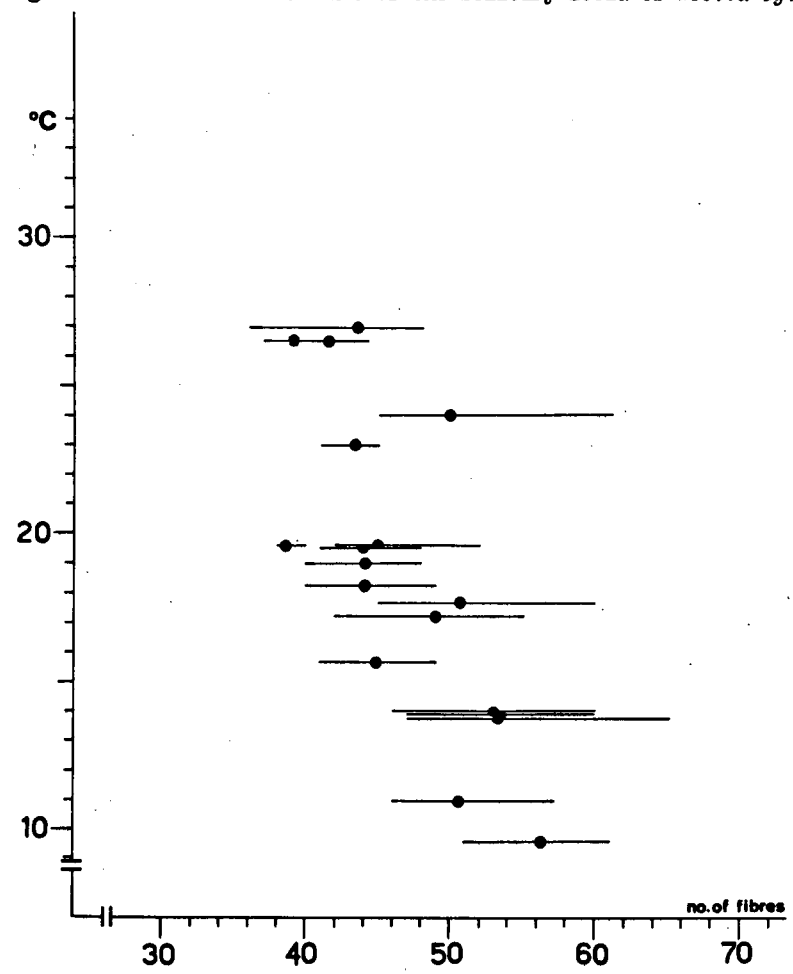

Fig. 12 Relation between sea surface temperatures (ordinate) and the mean and range of the total number of muscle fibres of the oral muscles (abscissa) in aggregate *Salpa fusiformis* samples from the three major oceans.