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Latitudinal variation in Atlantic *Salpa fusiformis* Cuvier, 1804 (Tunicata, Thaliacea)

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ABSTRACT

The existence of clinal variation in some morphological characters of Atlantic *Salpa fusiformis* Cuvier, 1804, is reported. The number of muscle fibres of both aggregate and solitary individuals is subjected to a decrease from higher to lower latitudes. Size and reproduction also seem to vary according to the latitude. The results and their bearing on infraspecific salp taxonomy are provisionally discussed.

INTRODUCTION

The holoplanktonic Salpidae are a group of animals with relatively few genera and few species, each of which has a wide, often worldwide distribution. *Salpa fusiformis* Cuvier, 1804, is the most widespread of all, occupying a range from 70° N to 40° S in the Atlantic Ocean and a similar distribution in other oceans. Formerly it was considered a species with two varieties or formae but without clear subspecies. Recently, however, Foxton (1961) separated three species on the basis of such characters as the number of muscle fibres, slight differences in the arrangement of the body muscles and the presence or absence of serrations of the test. The redescribed species *Salpa fusiformis* sensu Foxton (1961) has an almost cosmopolitan distribution besides being apparently monotypical, which seems a rather uncommon phenomenon, even in holoplanktonic animals. It seemed worthwhile to examine the variation of certain morphological characters of this species in detail.

Material was used from various oceanic localities, collected during several cruises of different vessels; all stations are plotted on the map of fig. 1 and listed in table I. My sincere thanks are due to the captains and crews of the naval vessels HMS "Luymes" and HMS "Snellius", and the fisheries research

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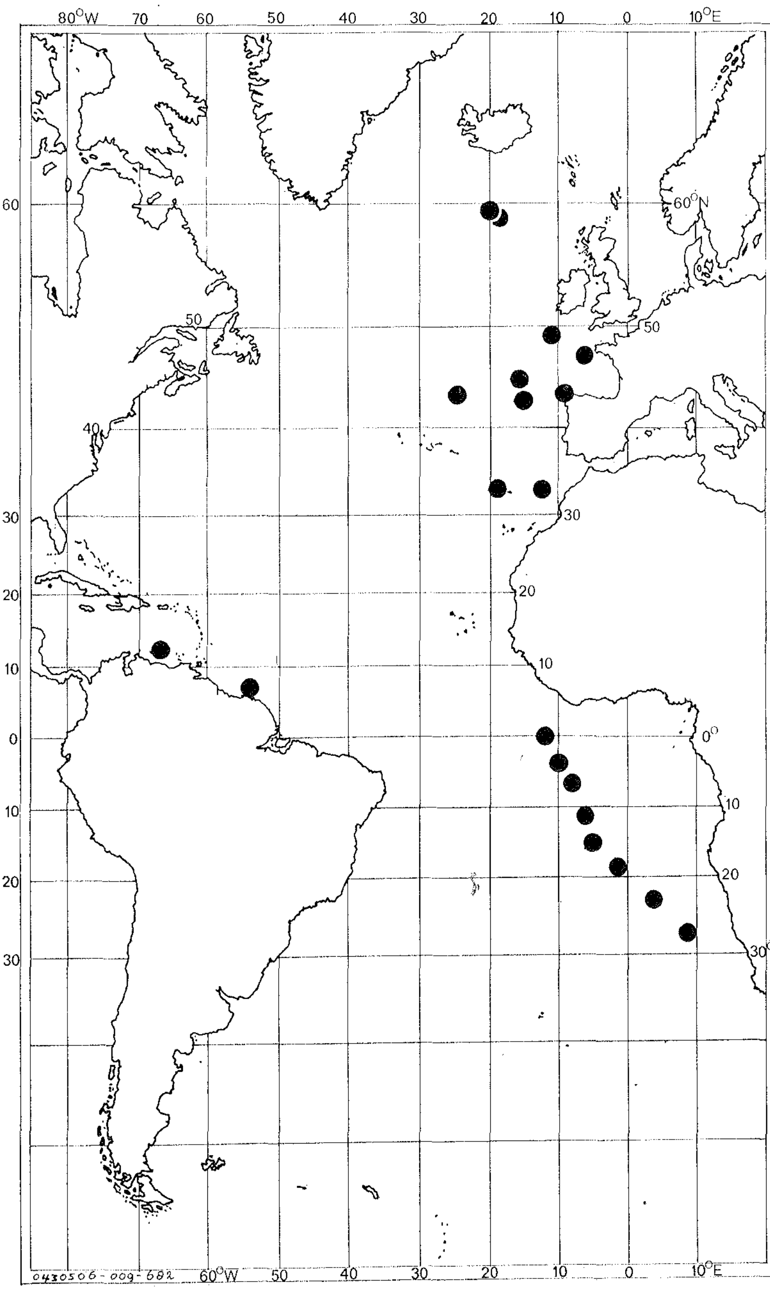

FIG. 1. Localities from which specimens of *Salpa fusiformis* were studied.

TABLE I. List of oceanic stations from which samples were studied.

Station	Position	Date	No. of sol.	No. of greg.
Cirrus IX	59°30 N, 20°00 W	VIII—1965	15	29
Cirrus VII	59°00 N, 19°00 W	VI—1964	5	6
Cirrus VI	45°00 N, 16°00 W	IV/V—1964	13	40
Tridens 12	49°00 N, 11°27 W	VI—1972	—	8
Tridens 4	43°30 N, 09°44 W	V—1972	8	12
Tridens 2	47°31 N, 06°59 W	V—1972	—	10
Snellius Navado III	ca 43° N, 25° W	VIII—1965	3	5
Cirrus "Kilo"	ca 42° N, 16° W	—	—	5
Snellius India 1	33°53 N, 12°55 W	IV—1965	2	3
Snellius India 2	33°52 N, 19°20 W	IV—1965	5	14
CICAR 16/17	6° N, 53° W	X—1970	2	12
CICAR 12B/13/14/15/18	ca 12° N, 68° W	IV/IX—1970	10	5
Dana 4000 VII/XI	00°31 S, 11°02 W	III—1930	2	7
Dana 3999 III	03°45 S, 10°00 W	III—1930	—	8
Dana 3998 II/XI	07°34 S, 08°48 W	III—1930	5	—
Dana 3997 V	11°00 S, 07°36 W	II—1930	10	2
Dana 3996 V	15°41 S, 05°50 W	II—1930	—	10
Dana 3981 IV/V	19°16 S, 01°48 W	II—1930	—	4
Dana 3980 IV	23°26 S, 03°56 E	II—1930	1	—
Dana 3979 III/V	27°10 S, 08°59 E	II—1930	—	4
		total	81	184

vessel R.V. "Tridens", and to Mr. C. L. Bekkering and Mr. S. Koning of the weatherships "Cirrus" and "Cumulus". The author is indebted to Dr. J. Knudsen of the Zoologisk Museum of Copenhagen for giving the opportunity to study material of the Dana-expeditions. I wish to express sincerest gratitude to Dr. P. Foxton (National Institute of Oceanography, Great Britain) for allowing me to study and publish some of his data, and for critically reading my manuscript.

Of the formalin preserved specimens the total body length (test included) and the width of each body muscle were measured. The number of fibres of each body muscle was counted following Foxton (l.c.). Also attention was paid to the development of stolon and embryo.

RESULTS

The results are summarized in fig. 2, table II a and b, and table III a and b.

Muscle fibres:

The total number of muscle fibres is not correlated with age or growth of the individuals as Foxton (1961) clearly showed. Present observations also failed to indicate any relation between the number of muscle fibres and size. Consequently it is not necessary to allow for age and growth when comparing the number of muscle fibres of *Salpa fusiformis* in different parts of the Atlantic.

TABLE II a. Ranges and means of the number of muscle fibres in solitary individuals from different latitudes and latitudinal ranges.

Latitude		Mean number of muscle fibres		No. of specimens	Range
59°30/59°	N	248.0		16	215—281
45°	N	247.0		10	228—278
43°	N	247.5		10	206—280
total		247.6	MIV: 22—40	36	206—281
33°	N	207.0	MIV: 21—25	5	193—241
12°	N	154.0		10	131—181
06°	N	159.5		2	157—162
00°		172.0		2	162—182
07°	S	154.0		5	140—172
11°	S	166.0		10	149—189
total		160.0	MIV: 13—22	29	131—189
23°	S	228.0	MIV: 26	1	—

TABLE II b. Ranges and means of the number of muscle fibres in aggregate individuals from different latitudes and latitudinal ranges.

59°00/59°30	N	59.6	32	50—68
49°	N	63.7	8	60—66
47°	N	56.7	10	52—61
45°	N	52.4	43	44—58
43°	N	56.3	16	46—65
42°	N	56.0	6	53—58
total		56.3	115	44—68
33°	N	40.3	16	36—45
12°	N	31.3	5	34—36
06°	N	35.0	11	26—34
00°		34.0	7	31—39
03°	S	36.1	8	33—39
11°	S	32.0	2	31—33
15°	S	35.0	10	31—38
19°	S	34.0	4	32—35
total		34.4	47	26—39
27°	S	42.3	4	40—46

A decrease in the total number of muscle fibres of M I—VI of aggregate individuals and of M I—IX of solitary specimens is clearly shown in fig. 2. The number of muscle fibres in aggregates seems to decrease more or less gradually from about 60 in the area northwest of Scotland to 30—35 in the Caribbean and the northern part of the South Atlantic Ocean. A few specimens from 27° S again have a higher number of 40—45. The same variation pattern is found in the solitary specimens. The number of muscle fibres

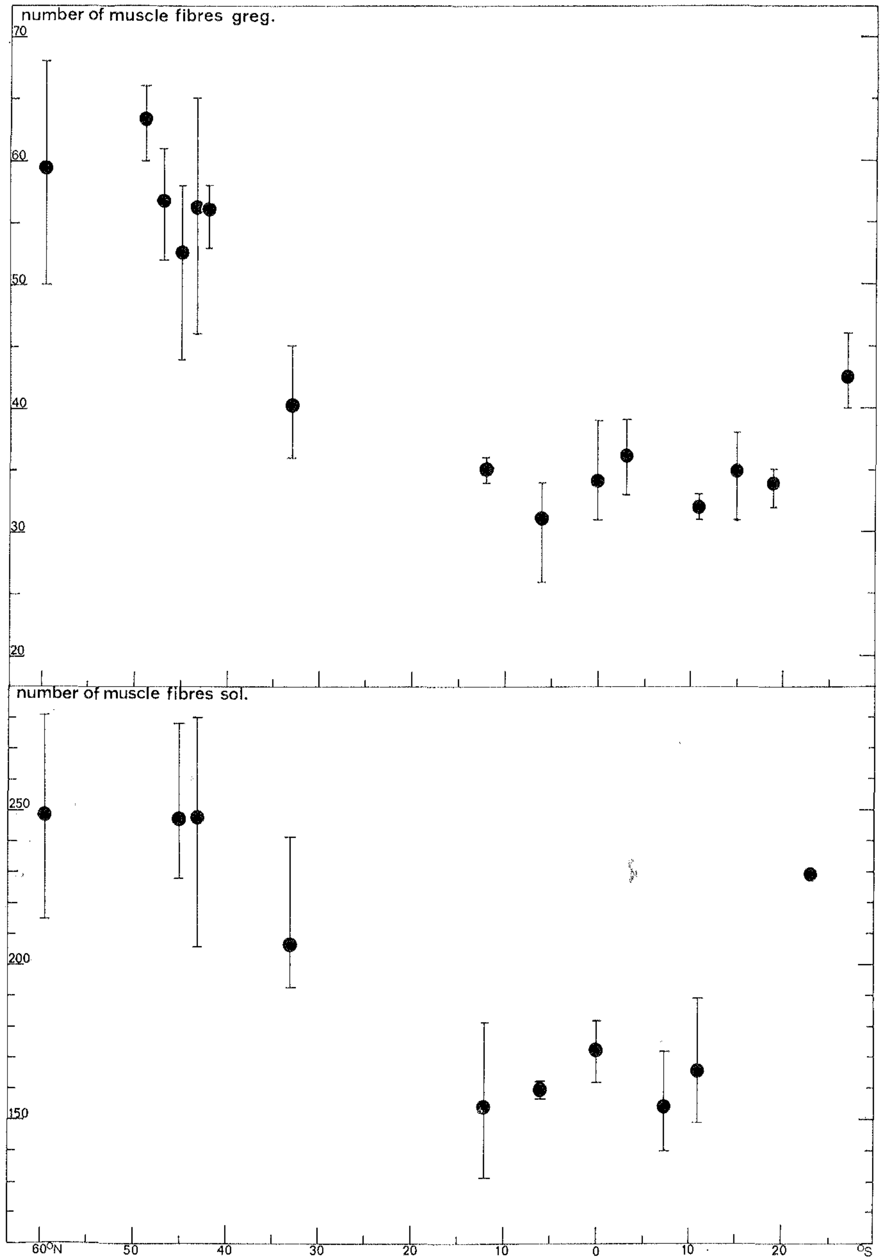

FIG. 2. Means (dots) and ranges (vertical bars) of muscle fibre numbers of aggregate (above) and solitary (beneath) *Salpa fusiformis* specimens plotted against latitudinal positions.

TABLE III a. Biometric differences between tropical (12° N—19° S) and northern (42°—60° N) solitary *Salpa fusiformis*.

	Tropical	Northern
Length (mm), largest	24.7 (n = 29)	52.0 (n = 36)
smallest *)	9.0 (n = 29)	22.1 (n = 36)
Smallest releasing specimens (mm)	16.5—20.0 (n = 29)	23.4—26.6 (n = 36)
Largest stolon individual (mm)	0.9 (n = 29)	2.4 (n = 36)
Muscle width, as % of body length,		
mean	26.1% (n = 13)	30.6% (n = 25)
range	23.1—31.1	25.4—39.9

*) i.e. specimens without remnants of elaioblast.

TABLE III b. Biometric differences between tropical (12° N—19° S) and northern (42°—60° N) aggregate *Salpa fusiformis*.

	Tropical	Northern
Length (mm), including projections,		
largest	14.9 (n = 49)	52.0 (n = 132)
smallest	6.5 (n = 49)	7.1 (n = 132)
Largest embryo (mm)	(0.5) (n = 49)	17.5 (n = 132)
Muscle width, as % of body length,		
mean	6.8% (n = 16)	10.6% (n = 73)
range	4.5—8.9	6.0—14.6

decreases from about 250 in the north to about 160 in tropical waters; one specimen from 23° S has 228 muscle fibres, which suggests a rise in the number towards southern latitudes. Unfortunately no material from more southern stations was available. However, it is to be expected that the number of fibres will still increase towards more southern regions, possibly to the same level as in the north. For the description of the four species of the so called *Salpa fusiformis* group Foxton (l.c.) only uses the number of muscle fibres of the fourth body muscle in solitary animals. To make comparison with his figures possible also the numbers of fibres of M IV in different areas are given.

Size:

From the available material it was difficult to establish a clear picture of the average size of the individuals of the populations residing in different areas. The average size of the specimens of the various samples under study would be of little value as this is influenced by the developmental stage of the population at the moment of capture. To trace size differences between the individuals of different populations one needs to study the life cycles of these populations and this necessitates rich samples, preferably covering all seasons, and these were not available. However, some measurements taken from the present material, though not being conclusive in themselves, give strong indications in this respect. In table III a and b the biggest and smallest specimens occurring in the samples from tropical and northern waters are compared. The maximum length in both solitary and aggregate specimens is considerably greater in northern than in tropical waters. Release of the first stolon block takes place at a smaller size in the tropics than in northern waters, while the individual size of zooids on the stolon is larger in northern than in tropical specimens. These observations strongly indicate that the number of muscle fibres as well as size (probably correlated with it) decrease from higher to lower latitudes.

Muscle width:

In contrast to the number of muscle fibres the width of each muscle and consequently the width of all muscles together depends on growth; a linear correlation of muscle width and body size is clear. In order to make comparable the total muscle width of individuals of different size it can be expressed as a percentage of the total body length

$$\frac{(\text{width of muscle I—VI (IX)} \times 100)}{\text{total length}},$$

although it is not a very accurate index, because body length is not in linear correlation to body size. This percentage was calculated for the tropical material from 12° N to 19° S and the boreal material from 42°—60° N; the results are given in table III a and b. The northern specimens, as expected, tend to have a relatively greater muscle width than tropical specimens.

Discussion

Attaining bigger size in colder water must obviously be an advantage for planktonic animals as this phenomenon is also found in other animal groups living in the surface waters of the open ocean, e.g. pteropods (van der Spoel, 1970). It also seems logical that bigger *Salpa fusiformis* should develop more muscle elements to meet their increase in size; this increase of muscle fibres results in an increase in width of the body muscles disproportionate to the increase in length of the animals (table III).

In the redescription of *Salpa fusiformis* by Foxton (1961) the number of muscle fibres is considered a distinctive character. For aggregate individuals he gives a number of muscle fibres of 40—61 (av. 51.8) and for solitary specimens the number of M IV is given as 19—40 (av. 29.4). Foxton (l.c.) used for the description specimens from all over the Atlantic Ocean. In the material upon which the present study is based the number of muscle fibres in aggregates appeared to vary from 26 to 68 and of M IV of solitary animals from 13 to 40, so the figures given by Foxton (l.c.) must be amended slightly. It seems also apparent from the present study that the average numbers given by him do not have distinctive value unless the region from which they were calculated is known. The value, as demonstrated by Foxton (l.c.), of the number of muscle fibres for the discrimination between *Salpa fusiformis* and its nearest relatives is not altered by the above considerations.

When the clinal variation presented here is viewed in detail one has to conclude that it is discontinuous. In the areas of 42°—60° N and 12° N—19° S the number of muscle fibres is rather constant. Between these areas and

TABLE IV. Countings of muscle fibres of *Salpa fusiformis* done by Dr. P. Foxton (National Institute of Oceanography, Great Britain), kindly offered for use in the present study.

Position	No. of specimens	Average No. of muscle fibres
63° N, 16° W	1 aggregate	61
	4 solitary	MIV: 37
47° N, 06° W	1 aggregate	56
	13 solitary	MIV: 32
44° N, 16° W	19 aggregate	54½
	11 solitary	MIV: 30
32° N, 09° W	6 aggregate	56½
32° N, 65° W	1 solitary	MIV: 23
14° N, 25° W	1 aggregate	40
33° S, 02° E	1 aggregate	44
34° S, 16° E	1 aggregate	41
35° S, 00°	2 solitary	MIV: 25
36° S, 00°	1 aggregate	43
38° S, 49° W	1 aggregate	49

south of 19° S intermediate numbers are found. This distribution of characters strongly coincides with the distribution of oceanic regions such as those proposed by for instance Steuer (1933), who based his subdivision on the distribution of copepods. The area of 42°—60° N with average muscle fibre numbers of 247/57 corresponds with his Northern Subarctic Region; the stations at 33° N with average muscle fibre numbers 207/40 correspond with his Northern Subtropical Subregion; the stations between 12° N and 19° S with average muscle fibre numbers 160/34.5 fall within his Tropical Region. The region in which the stations at 23° S and 27° S (respectively —/228 and 42/—) should be localized is uncertain (either his Southern Subtropical Subregion or the Benguela area), but they lie outside his Tropical Region. Amor (1966) gives for aggregate *Salpa fusiformis* from the area between 33° and 40° S along the South American coast a muscle fibre number of 41; this area also lies outside Steuer's Tropical Region. Oceanic subregions proposed by other authors differ on minor grounds from the division made by Steuer (l.c.), but are also in agreement with the observed distribution of *Salpa fusiformis* characters. A few Mediterranean specimens (n = 29) from 37°—43° N of *Salpa fusiformis* have also been studied. The mean number of muscle fibres of aggregate specimens appeared to be 48.5, of solitary animals 216. These values are intermediate between northern and subtropical numbers.

Dr. Foxton most kindly sent me the results of the countings of muscle fibres of his *Salpa fusiformis* specimens to add to and compare with my figures. They are listed in table IV. The countings conform largely with those from my own specimens except for the specimens from 32° N, 09° W (Discovery Station 3297). The six aggregate specimens have a high number of muscle fibres compared to the 16 specimens collected by HMS "Snellius" at 33° N, 12°—19° W. This discrepancy seems to be inexplicable. The area should be studied more extensively to assess the variation in the number of muscle fibres of the residing *Salpa fusiformis* population.

In all, *Salpa fusiformis*, seems to have distinct separate populations within each region, the individuals of which are each characterized by a limited variation in the number of muscle fibres, and a size-growth-reproduction relation differing meristically from that of individuals in neighbouring regions. These observations suggest that the differences are caused, not merely by ecological adaptation, but by a certain degree of genetical difference which arose by a restriction of gene flow, as mixing of watermasses and their plankton populations is probably restricted to small boundary areas between the watermasses. The forma-concept of van der Spoel (1971) might cover the observed phenomena. In his opinion some groups of populations of oceanic plankton species live separated from each other because their respective habitats do not mix apart from bordering areas and they develop diversity as a result of changing selective pressure of the 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 distinctly differing phenotypes, while the boundary populations would show intermediates between the "formae". Though the differences between the formae are slight and often merely biometric it seems nevertheless useful to name them and give them taxonomic status because they are in contrast to the species as a whole restricted in their distribution to a certain watermass or region. Whether or not formae sensu van der Spoel exist in Atlantic *Salpa fusiformis* is hard to decide from the present material since critical geographic areas remain unsampled. The decision whether to name and describe any infraspecific groups of populations of this species must therefore be postponed until more Atlantic material and also material from other oceans has been examined.

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