

LATITUDINAL VARIATION OF THE NUMBER OF MUSCLE
FIBRES IN *SALPA THOMPSONI* (TUNICATA, THALIACEA)
IN THE SOUTHERN OCEAN: IMPLICATIONS FOR THE
VALIDITY OF THE SPECIES *SALPA GERLACHEI*

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Abstract: The latitudinal variation is of common occurrence in epiplanktonic species with a wide north-south distribution. In Salpidae this phenomenon has been observed in the number of fibres of the body muscles, which is uniform in all tropical-temperate water species. Nevertheless, up to now it has not been observed in species restricted to the Southern Ocean.

In this paper we discuss the existence of latitudinal variation in *Salpa thompsoni*, which is widely distributed and the most abundant salp species in the Southern Ocean.

The number of muscle fibres of both aggregate and solitary forms of *S. thompsoni* showed a maximum at about 56°S and decreased gradually towards the higher latitudes. Body length varied latitudinally the same as the fibre numbers did. In the high latitudes of the Pacific Sector of the Southern Ocean, *S. thompsoni* is replaced by a sibling species, *Salpa gerlachei*. These two species differ only biometrically in fibre numbers per muscle band, being less in *S. gerlachei*. However, a broad overlap in the range of muscle fibre numbers was found between the two species. The present results suggest that these two species are synonymous and *S. thompsoni* is distributed with a clinal variation from the north to the south.

1. Introduction

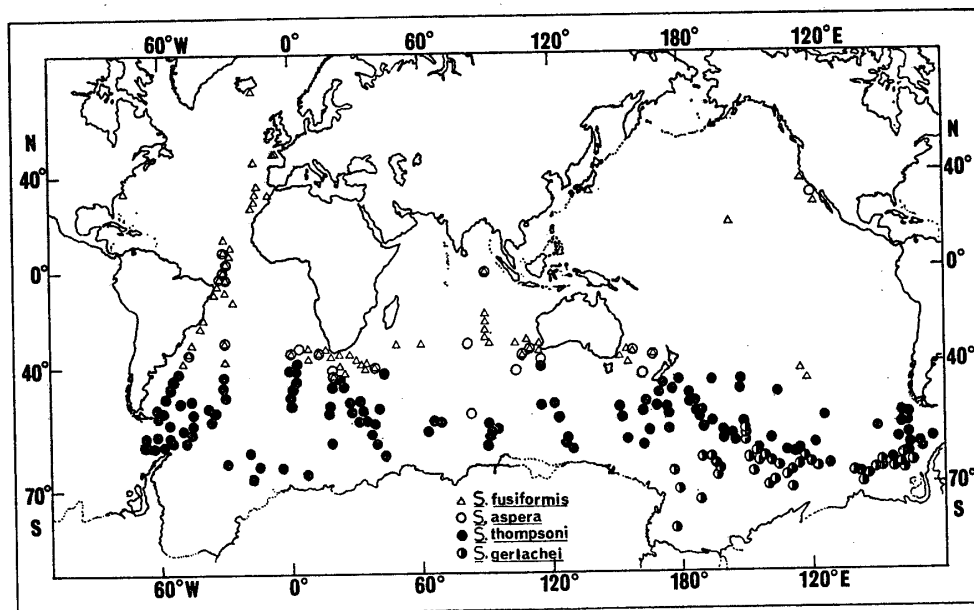
The latitudinal variation is commonly observed in epiplanktonic species with a wide north-south distribution. In Pteropoda (SPOEL, 1967, 1974) such a north-south variation, concerning shell form and dimensions, has been reported for *Clio pyramidata*, *Limocina helicina* and *Cavolinia tridentata*. The Copepoda *Eucalanus bungii* shows latitudinal variation in the North Pacific (FLEMINGER and HULSEMAN, 1973), as does the Euphausiacea *Thysanoessa longipes* (BRINTON, 1962). In Chaetognatha, the clinal variation in the number of teeth has been described for *Sagitta serratodentata* (PIERROT-BULTS, 1976) and *S. elegans* (RITTER-ZAHONY, 1911 after PIERROT-BULTS, 1976). The Pyrosomata *Pyrosoma atlanticum* varied latitudinally in the number of branchial stigmata (probably only in Indo-Pacific waters) (SOEST, unpublished data). In salps, a latitudinal variation is also observed in the number of body muscle fibres (SOEST, 1972, 1973, 1974, 1975a, b; ESNAL *et al.*, 1983; VISSER and SOEST, 1987).

The muscle bands, characteristic of Salpidae, are composed of muscle fibres

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arranged parallel to each other and to the main axis of the muscle band. The arrangement of the body muscles as well as the number of fibres per muscle band are very useful taxonomical characters. Nevertheless, the latitudinal variation in the number of muscle fibres has been found in all eurythermal species; more in number in the northern and southern temperate and subantarctic-subarctic waters, less in number in tropical waters and intermediate numbers in subtropical waters. The species concerned are: *Salpa fusiformis*, *S. aspera*, *S. maxima*, *Thalia democratica*, *Iasis zonaria*, *Ihleia punctata*, *Pegea confoederata*, *Thetys vagina*, *Cyclosalpa pinnata*, *C. bakeri* and *Helicosalpa virgula*.

The latitudinal variation of salps in the Southern Ocean has not been studied yet. Among the species in this area, *Salpa thompsoni* is widely distributed around Antarctica, extending from the Subtropical Convergence to the pack-ice zone. In the high latitudes of the Pacific Sector, *S. thompsoni* is replaced by a closely related species, *Salpa gerlachei*. This species occurs south of 65°S and between 175°E and 80°W. *S. gerlachei* is the only Antarctic species that does not have a circumpolar distribution (FOXTON, 1966) (see Fig. 1).



Foxton, 1961

Fig. 1. Distribution of *S. fusiformis*, *S. aspera*, *S. thompsoni* and *S. gerlachei*. After FOXTON, 1961.

In 1961, FOXTON classified *S. thompsoni* and *S. gerlachei* from a single species *Salpa fusiformis aspera* on the basis of biometrical characters such as the number of fibres per muscle band and the relation between body length and muscle width. The two species are identical morphologically other than the biometrical difference.

CALDWELL (1966) and ESNAL (1970) found many specimens of *S. thompsoni* with intermediate number of muscle fibres and consequently they described the difficulty of the identification of the two species.

The present study is to propose a possible latitudinal variation pattern in the number of muscle fibres for the species *S. thompsoni* and to discuss the taxonomic

validity of the species *S. gerlachei*.

2. Materials and Methods

Samples were collected from various localities of the Southern Ocean during the following cruises: KH-68-4 cruise (Southern Cross Cruise) of R. V. HAKUHO MARU (Ocean Research Institute, University of Tokyo) from November 1968 to March 1969 in the Pacific Sector (between 155°E and 170°W); KH-83-4 cruise (BIOMASS SIBEX I) of the same vessel from November 1983 to February 1984 in the Australian Sector and BIOMASS SIBEX II cruise of R. V. KAIYO MARU (Japan Fisheries Agency) from October 1984 to February 1985 in the Pacific Sector (about 90°W), Drake Passage and Atlantic Sector. The positions of the sampling stations are indicated in Fig. 2 and listed in Table 1.

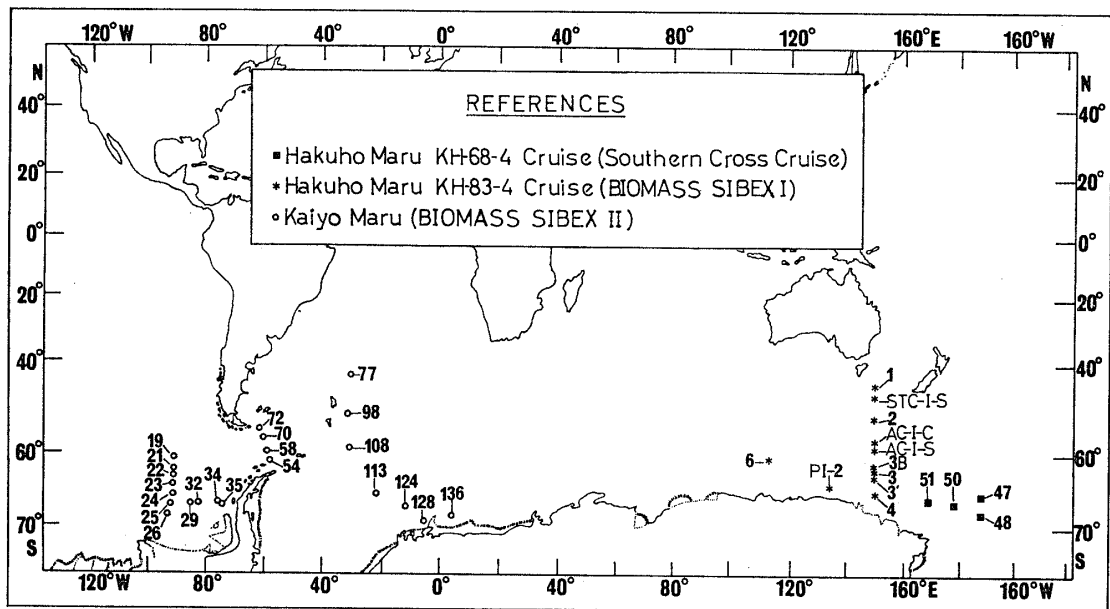


Fig. 2. Study area and the position of stations where samples were available.

More than 800 specimens of *S. thompsoni* were studied (500 of the aggregate form and 350 of the solitary form). All samples were preserved with formaline solution. The number of muscle fibres was counted following FOXTON (1961): for the aggregate form, the total number of muscle fibres (from Muscle I to Muscle VI) was counted because there is considerable variation in the numbers from muscle to muscle; for the solitary form only the number of muscle fibres of Muscle IV was counted, as it has very high fibre counts in all (nine) body muscles. Muscle IV is convenient for specific identification because it is easily found and in general is well preserved due to its central position.

For both forms the standard body length (distance between the mouth and the atrial opening) and the width of Muscle IV were measured. Aqueous staining by Bengal Rose was employed to facilitate the observation of muscle bands and counts of muscle fibres.

Table 1. List of sampling data.

Cruise	Station	Position	Date	Net type	Sampling layer (m)
KH-68-4	47	66°00.0'S, 170°00.0'W	1969, Jan. 17	Norpac-xx13	0-148
	48	68 00.1 S, 170 06.9 W	Jan. 18	Norpac-xx13	0-147
	50	66 44.0 S, 179 56.6 E	Jan. 21	Norpac-xx13	0-145
	51	66 30.0 S, 170 08.0 E	Jan. 21	Norpac-xx13	0-150
KH-83-4	1	45 06.8 S, 150 09.9 E	1983, Dec. 14	10 ft-IKMT	0-1050
	2	52 07.4 S, 149 52.6 E	Dec. 16	10 ft-IKMT	0-905
	3	61 27.0 S, 150 29.6 E	Dec. 19	10 ft-IKMT	0-870
	4	64 56.4 S, 150 10.4 E	Dec. 21	10 ft-IKMT	0-670
	3B	61 25.6 S, 150 00.1 E	Dec. 26	10 ft-IKMT	0-860
	3'	61 32.3 S, 150 26.3 E	1984, Jan. 13	10 ft-IKMT	0-535
	PI-2	64 13.5 S, 135 43.1 E	Jan. 17	10 ft-IKMT	0-570
	6	60 00.3 S, 116 01.0 E	Jan. 22	10 ft-IKMT	0-862
	AC-I-C	56 12.2 S, 150 00.5 E	1983, Dec. 28	MTD-GG54	0, 11, 34, 56, 84, 112, 168, 224
	AC-I-S	56 23.2 S, 149 59.5 E	Dec. 28	MTD-GG54	0, 10, 31, 52, 78, 104, 155, 207
	STC-I-S	47 00.4 S, 150 00.4 E	1984, Jan. 1	MTD-GG54	0, 11, 34, 56, 84, 113, 169, 225
KAIYO MARU BIOMASS SIBEX II	21A	62 00.1 S, 89 56.5 W	1984, Dec. 3	KYMT	0-90
	22A	62 59.3 S, 89 58.4 W	Dec. 3	KYMT	0-103
	23A	64 01.8 S, 90 02.6 W	1984, Dec. 3	KYMT	0-127
	24A	65 29.4 S, 90 02.4 W	Dec. 4	KYMT	0-108
	25A	67 01.6 S, 90 35.9 W	Dec. 5	KYMT	0-80
	29B	66 35.6 S, 83 52.8 W	Dec. 6	KYMT	0-120
	34B	66 59.7 S, 74 55.1 W	Dec. 8	KYMT	0-145
	35B	67 01.7 S, 73 51.6 W	Dec. 8	KYMT	0-30~70 (aimed)
	46B	63 07.7 S, 64 02.9 W	Dec. 10	KYMT	no data
	77D	42 59.2 S, 29 59.9 W	1985, Jan. 4	KYMT	0-150
	98D	59 01.3 S, 30 02.1 W	Jan. 10	KYMT	0-115
	108D	61 09.1 S, 21 38.8 W	Jan. 12	KYMT	0-25~40 (aimed)
	128E	69 26.2 S, 04 15.2 W	Jan. 18	KYMT	0-18
	133E	68 46.2 S, 01 19.6 W	Jan. 20	KYMT	0-15~25 (aimed)
	136E	69 40.4 S, 05 35.9 W	Jan. 20	KYMT	0-37
	19A	61 01.3 S, 89 57.7 W	1984, Dec. 2	ORI-200	no data
	21A	62 01.9 S, 89 54.0 W	Dec. 3	ORI-200	0-144
	22A	62 58.3 S, 84 59.5 W	Dec. 3	ORI-200	0-125
	23A	64 01.1 S, 90 01.9 W	Dec. 3	ORI-200	0-180
	24A	65 29.2 S, 89 58.9 W	Dec. 4	ORI-200	0-157
	32B	66 41.0 S, 81 05.9 W	Dec. 6	ORI-200	0-109
	34B	66 59.7 S, 74 53.8 W	Dec. 8	ORI-200	0-172
	58C	66 59.2 S, 56 43.9 W	Dec. 14	ORI-200	0-146
	77D	43 00.1 S, 29 59.8 W	1985, Jan. 4	ORI-200	0-85
	98D	50 01.6 S, 30 02.8 W	Jan. 10	ORI-200	0-132
	113D	64 56.6 S, 20 01.2 W	Jan. 14	ORI-200	0-110
	24A	65 29.4 S, 90 02.4 W	1984, Dec. 4	ORI-300	side oblique (no data)
25A	67 01.3 S, 90 33.7 W	Dec. 5	ORI-300	"	
26A	67 37.9 S, 91 05.5 W	Dec. 5	ORI-300	"	
54C	60 58.5 S, 55 48.4 W	Dec. 13	ORI-300	"	
70C	56 20.2 S, 59 28.8 W	Dec. 16	ORI-300	"	
72C	55 40.9 S, 60 01.0 W	Dec. 16	ORI-300	"	

3. Results

3.1. Number of muscle fibres in relation with body length

The number of muscle fibres is not correlated with body length or developmental stage of the individuals as shown in Fig. 3a and 3b. At any body length or developmental stage (these developmental stages were already described in CASARETO and NEMOTO, 1986), the number of muscle fibres is nearly constant (mean \pm S.D.). Therefore, the number of muscle fibres can be used in taxonomical identification independent of the age of the animal. It was firstly suggested by BERRILL, 1950: he observed a

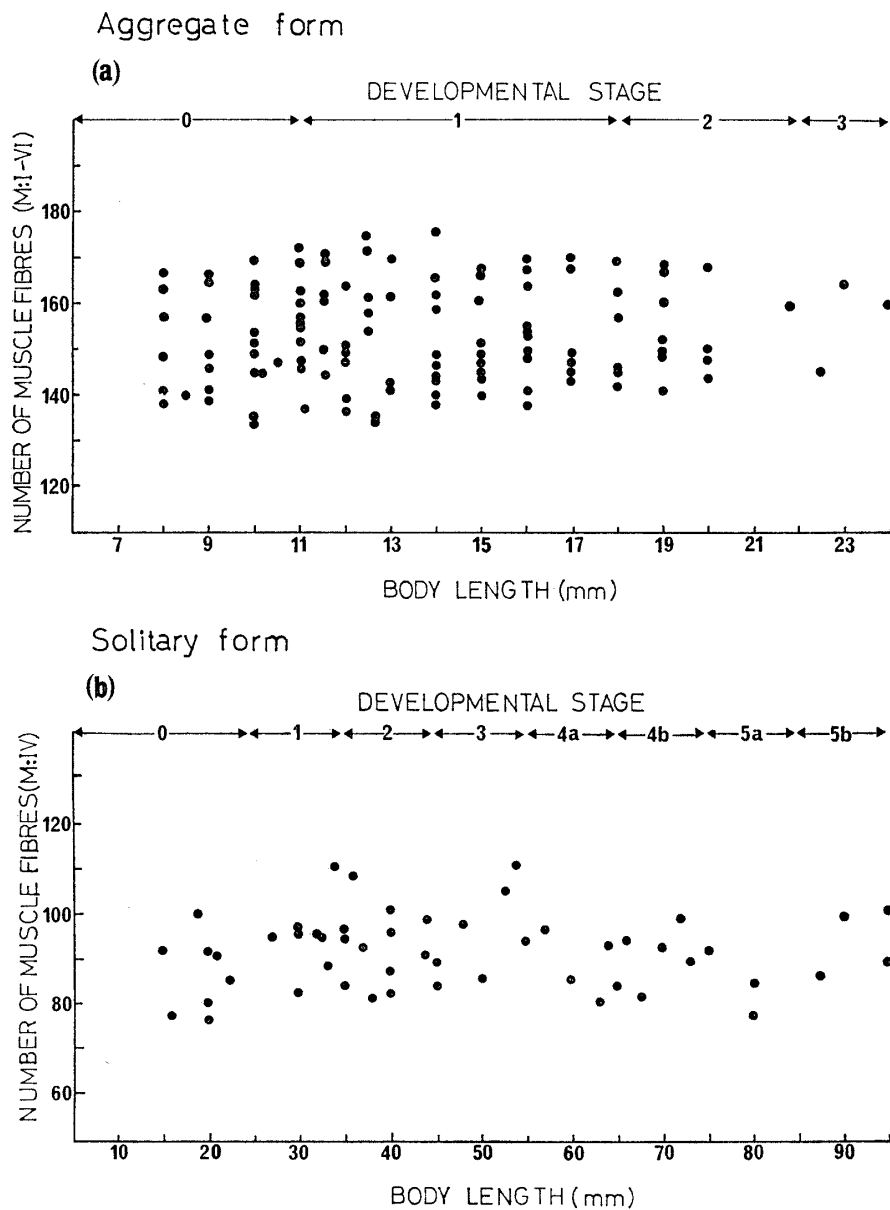


Fig. 3. Number of muscle fibres plotted against body length and progressive developmental stages of *S. thompsoni*. a) Aggregate form: total number of muscle fibres (from Muscle I to Muscle VI). b) Solitary form: number of muscle fibres of Muscle IV.

considerable difference in the number of muscle fibres of different species, and the number of rudimentary fibres firstly discernible in an embryonic stage or bud do not increase with age in the larger solitary or aggregate individuals.

3.2. Width of muscle band

Width of muscle band is of another importance, because the muscle fibres increase in width as the animal grows.

The significant linear correlation between the width of Muscle IV and the body length for both solitary and aggregate forms of *S. thompsoni* indicates that the width of muscle band itself increases proportionally with increasing body length (Figs. 4a and 4b). A constant ratio of body length/muscle width can be obtained for a given species. FOXTON (1961) used this ratio to distinguish *S. thompsoni* from *S. gerlachei*. The ratios observed in this study coincided with those given by FOXTON (*loc. cit.*) for the species *S. thompsoni* including those specimens collected within the supposed distributional area of *S. gerlachei*.

3.3. Number of muscle fibres, body length and the ratio of body length/muscle width in relation to latitude

Figure 5a shows the total number of muscle fibres of the aggregate form of *S. thompsoni* on the latitude using the data available (500 specimens). A maximum value is observed at about 56°S, then decreases gradually towards the higher latitudes. South of 56°S, a significant relation is observed with a regression coefficient of $r = -0.83$. In the case of the solitary form (Fig. 5b), the number of muscle fibres of Muscle IV was plotted against the latitude (350 specimens). The same variation pattern is observed: a maximum at about 56°S and a gradual decrease towards the south. The regression line is fairly significant ($r = -0.93$).

Table 2. Ratio of body length/muscle width at different latitudes for the solitary and aggregate forms of *S. thompsoni*. The number of specimens counted is represented in parenthesis.

Latitudinal range	45-46°S	52-53°S	55-56°S	59-60°S
Solitary form	24.40 (1)	23.1±3.1 (10)	23.69±3.2 (29)	24.24±3.4 (17)
Aggregate form	18.12±2.8 (16)	15.89±1.3 (10)	16.5±1.5 (53)	20.58±1.3 (93)
Latitudinal range	61-62°S	64-65°S	66-67°S	68-69°S
Solitary form	24.73±3.5 (23)	23.19±2.4 (4)	24.01±2.7 (3)	20.88±0.5 (7)
Aggregate form	17.77±2.7 (61)	19.37±2.8 (76)	20.9±2.6 (133)	19.98±2.7 (23)

The relationship between the body length and the latitude at each stage for both solitary and aggregate forms of *S. thompsoni* is represented in Figs. 6a and 6b. The same trends as the number of muscle fibres are observed in body length which increases around 56°S and gradually decreases towards the south.

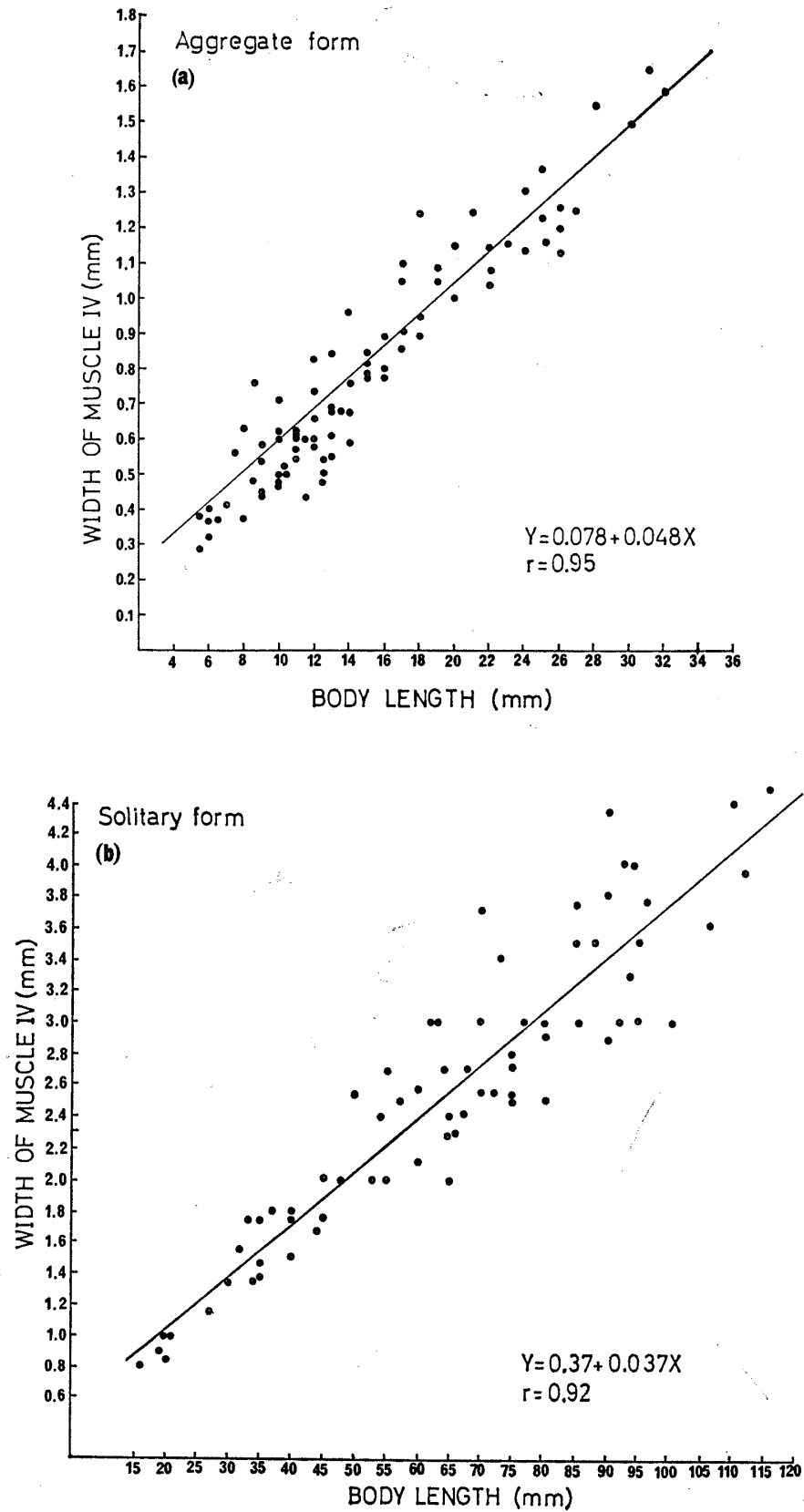


Fig. 4. Relationship between width of Muscle IV and body length of *S. thompsoni*. a) Aggregate form, b) Solitary form.

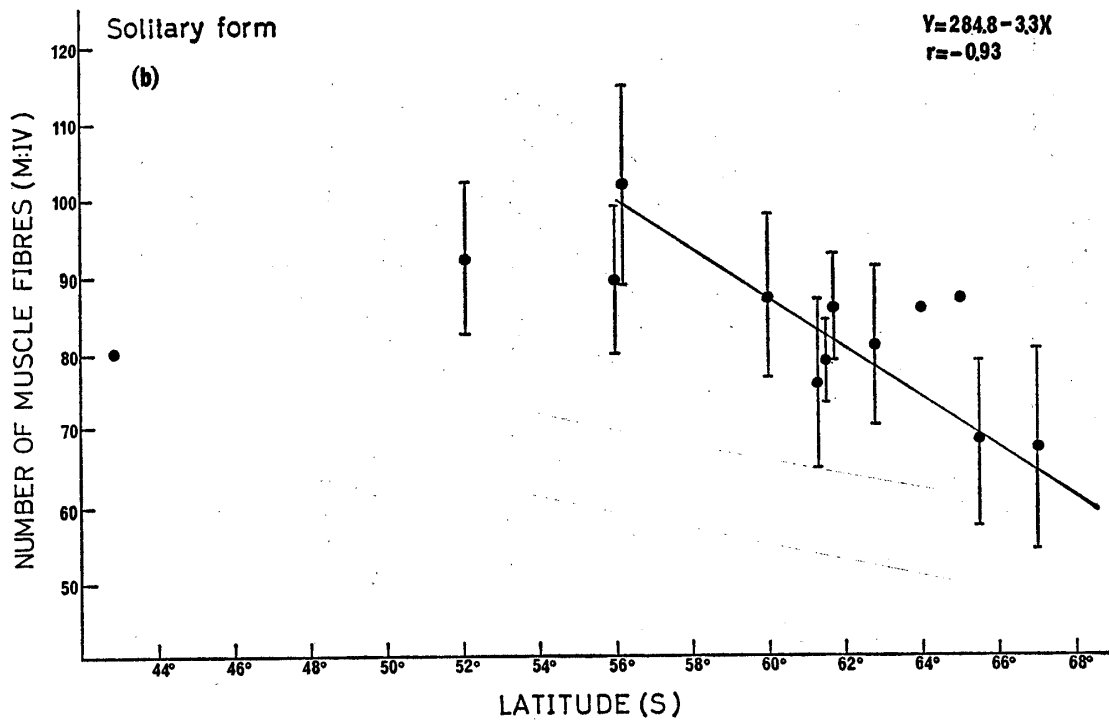
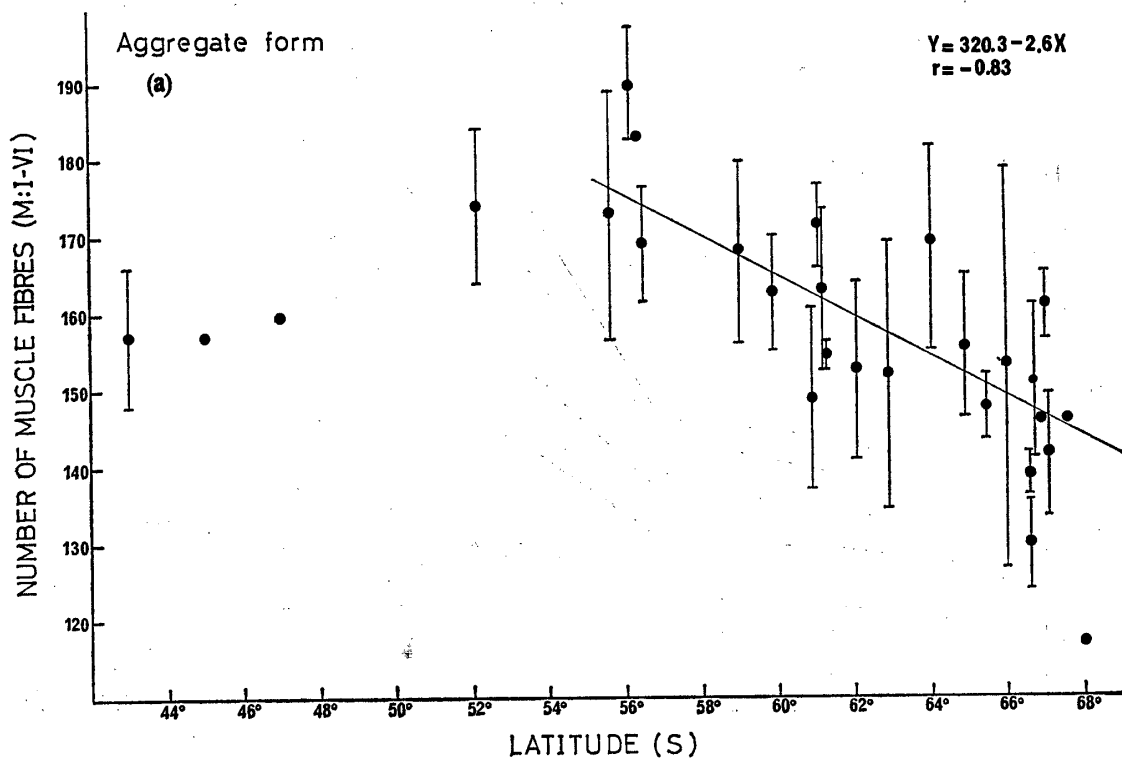


Fig. 5. Number of muscle fibres plotted against latitude of *S. thompsoni*. a) Aggregate form: total number of muscle fibres. b) Solitary form: number of muscle fibres of Muscle IV.

The ratios of body length/muscle width of both forms of *S. thompsoni* in eight latitudinal zones are listed in Table 2 which shows nearly constant values from the north to the south.

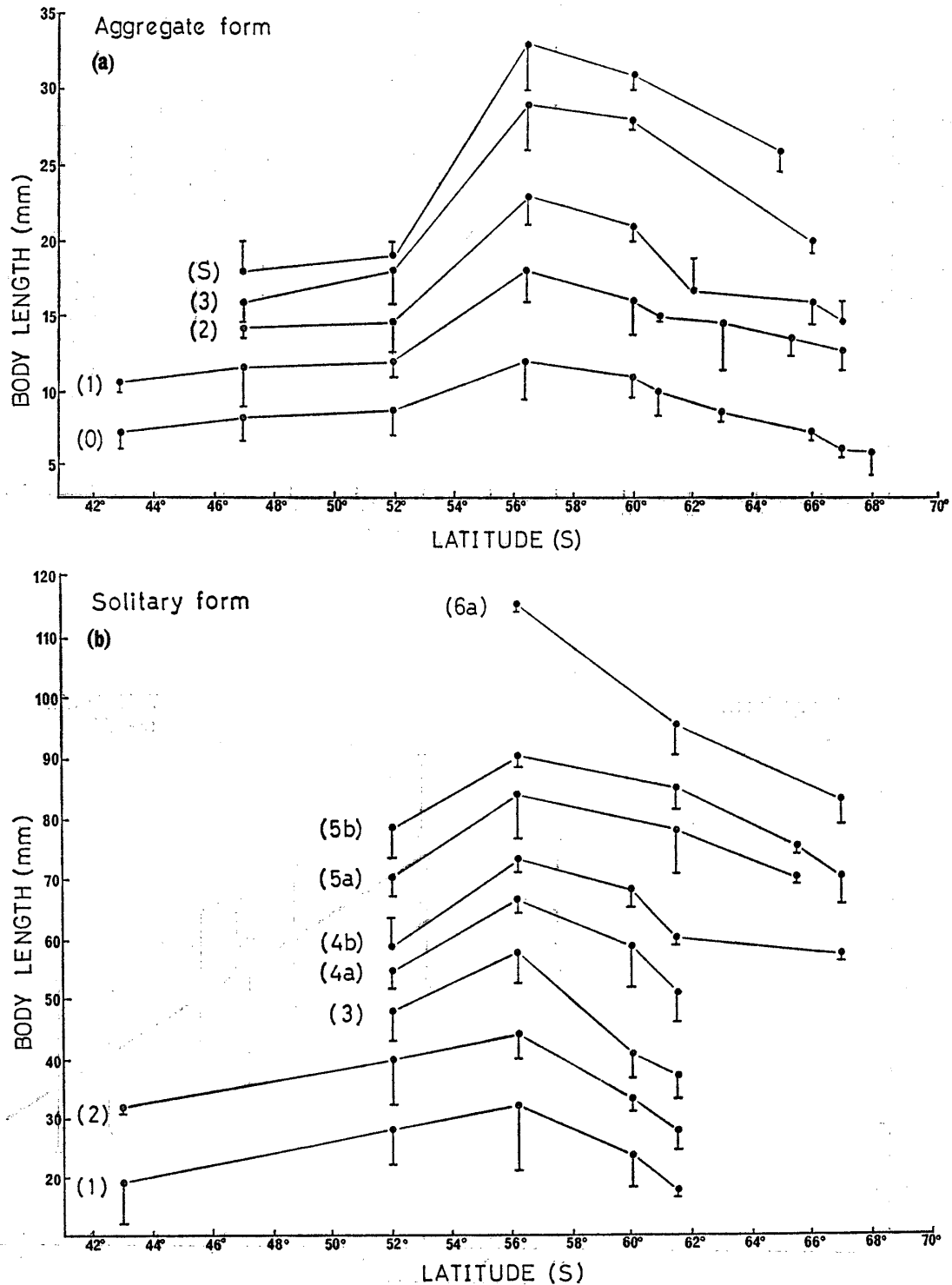


Fig. 6. Average body length plotted against latitude of *S. thompsoni*. a) Aggregate form: 0 (embryo), 1, 2, 3 and S (spent) indicate developmental stages. b) Solitary form: 1, 2, 3, 4a, 4b, 5a, 5b and 6a indicate developmental stages.

4. Discussion

SOEST (1975a) discussed the latitudinal variation in the number of muscle fibres of salps. He found the variation in several tropical-temperate water species from all the oceans and concluded that it is a universal trend in all salp species with a wide distribution. Figure 7 shows the typical pattern for the aggregate form of *Salpa fusiformis*, in which data are cited from SOEST (1975a) and compiled by the present authors. The numbers of muscle fibres in tropical waters were considerably less than those in temperate-subantarctic and subarctic waters.

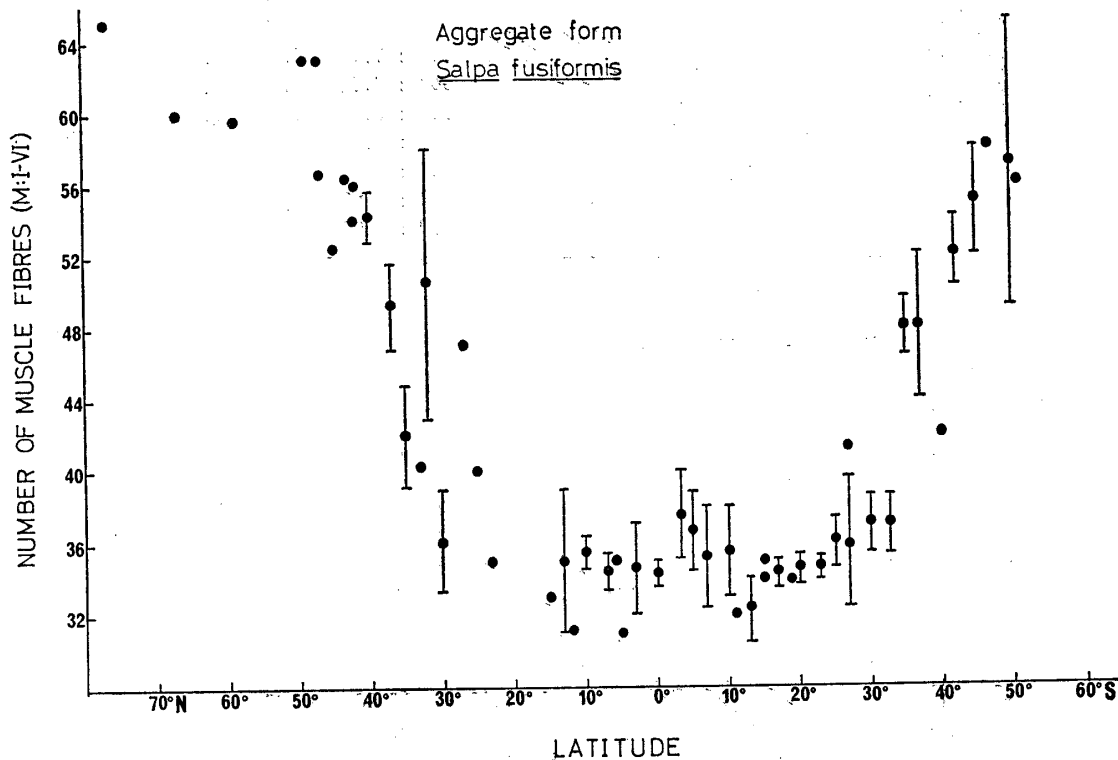


Fig. 7. Total number of muscle fibres (from Muscle I to Muscle VI) plotted against latitude for the aggregate form of *S. fusiformis* (data from SOEST, 1975a).

The latitudinal variation of widely distributed species such as *S. fusiformis* is quite different from that of *S. thompsoni*: for the tropical-temperate water species, the number of muscle fibres tends to increase at higher latitudes or in cold waters. In the case of *S. thompsoni*, however, at higher latitudes, the number of muscle fibres and the body length decrease gradually with increasing latitude in the Antarctic Ocean.

If the ratio of body length/muscle width is constant from the north to the south as shown in Table 2, the aspect of the animal in a certain developmental stage does not vary with latitude, although the body length of each maturity stage gradually decreases towards the south. Figures 8a and 8b show that the animal in each developmental stage has smaller body length, and thus the solitary population with relatively smaller body length at southern localities probably begins to release buds actively (from stage 4b). The relationship between the body length and the bud release described above

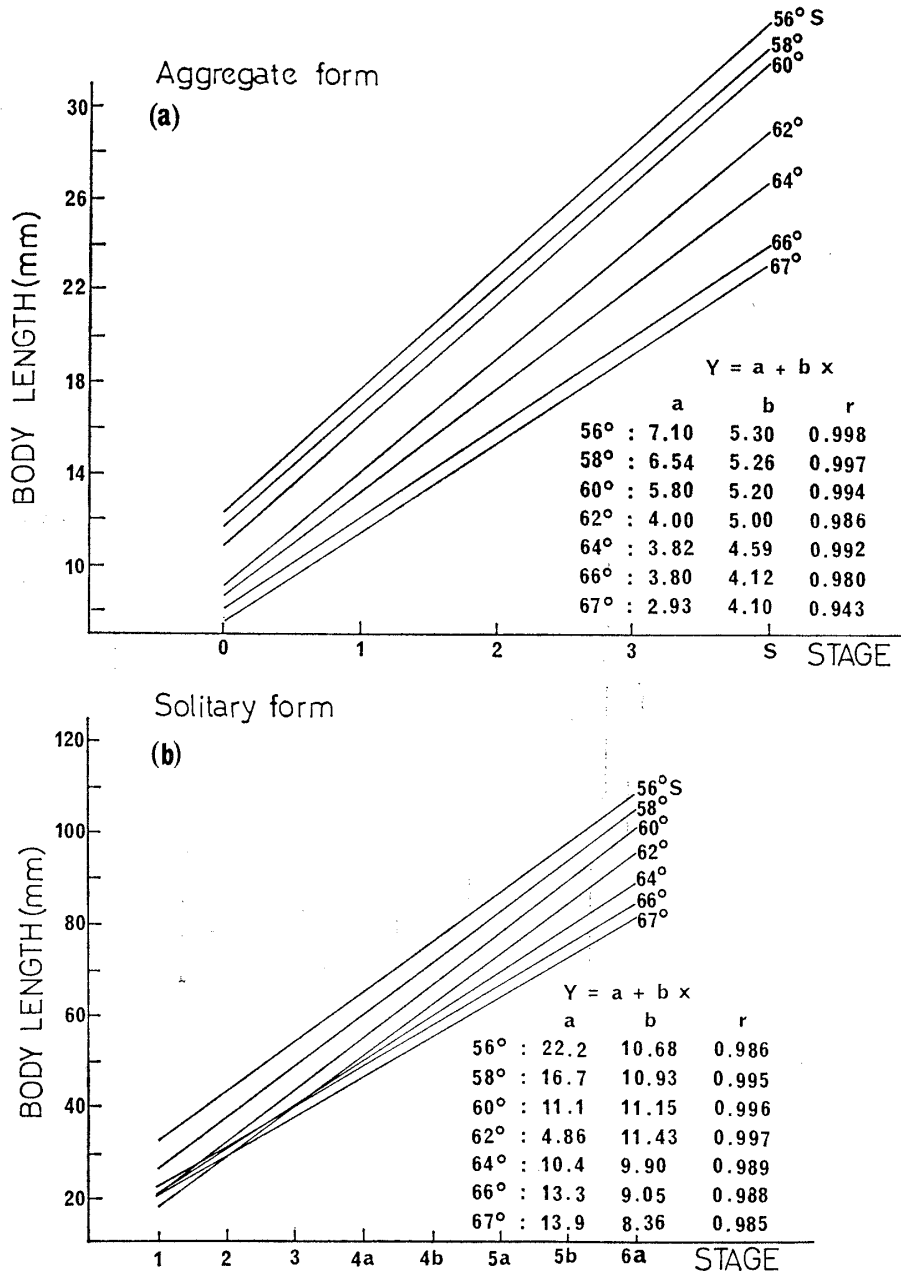


Fig. 8. Body length plotted against developmental stages of *S. thompsoni* at different latitudes. a) Aggregate form, b) Solitary form.

was firstly observed by FOXTON (1961, 1966). He studied the development of the stolon of the solitary population in *S. thompsoni* and *S. gerlachei* and compared body length and budding production at each developmental stage in both species. He observed *S. gerlachei* (sensu FOXTON) commences active bud release at a relatively smaller body length than *S. thompsoni*.

Growth rates of solitary and aggregate forms probably vary from the north to the south and within a year. It is well known that the swarming activity of salps is closely related to phytoplankton blooming (FOXTON, 1966; HERON 1972a, b; SILVER, 1975). At higher latitudes phytoplankton production is restricted to a short period of

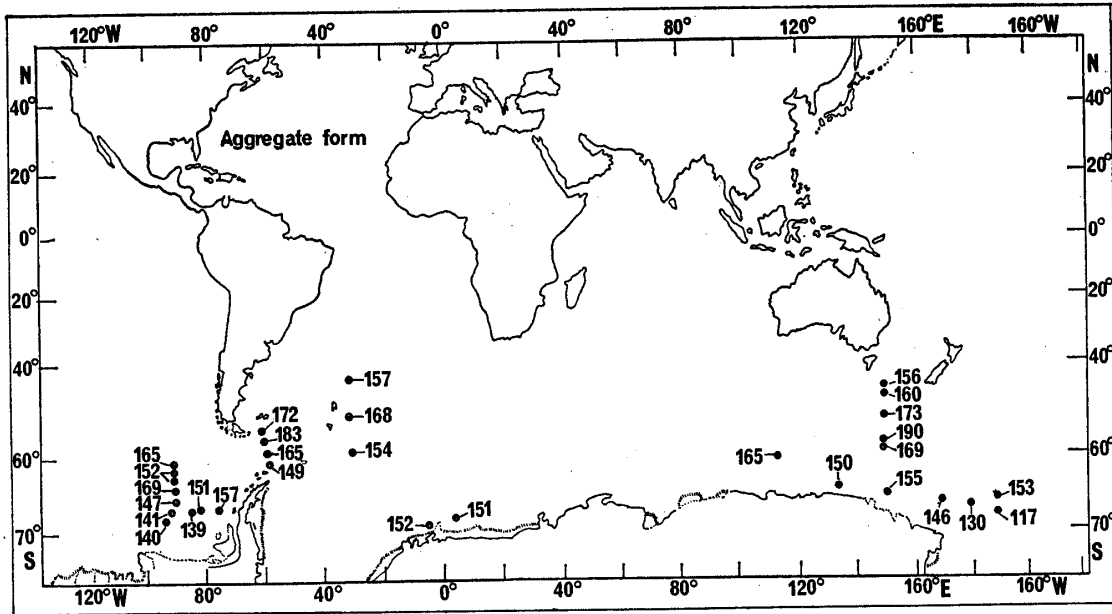


Fig. 9. Average number of total muscle fibres for the aggregate form of *S. thompsoni* at each station.

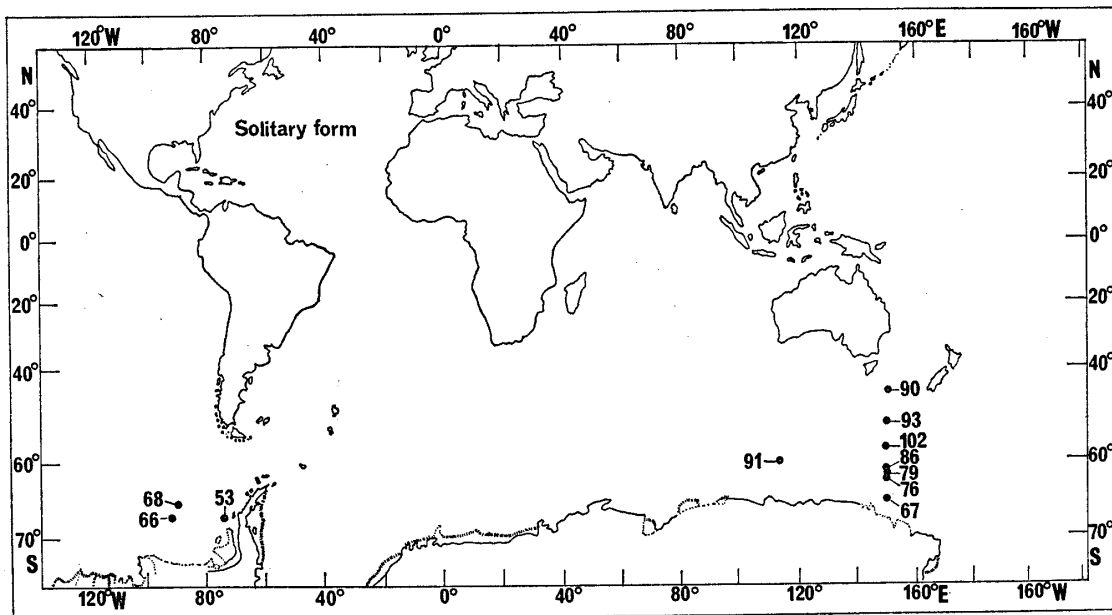


Fig. 10. Average number of Muscle IV fibres for the solitary form of *S. thompsoni* at each station.

time under enough light and therefore salps production would also be limited for time. The growth rate of salps should be faster at higher latitudes especially in summer than that at lower latitudes.

It is noticeable that the maximum number of muscle fibres occurred at about 56°S (Figs. 9 and 10), and that for the aggregate form the maximum number of muscle fibres occurred at 90°W (Stn. 23, 169 muscle fibres), eastern Drake Passage (Stn. 70, 183 muscle fibres) and 150°E (Stn. AC-I-C, 190 muscle fibres), where faster current speeds than in other stations were observed (see NAKAI *et al.*, 1985; NAGANOBU and

HISANAGA, 1986). Although less data are available for the solitary form, a maximum number of muscle fibres of Muscle IV (102) also occurred at 150°E at Stn. AC-I-C. Further investigation will be needed on responses of salps to an environmental condition such as current speeds with reference to their muscular system.

The latitudinal variation pattern for *S. thompsoni* opens a question on the validity in taxonomy of the species *S. gerlachei*. SOEST (1974, 1975a) suggested that *S. gerlachei* can be a clinal form of *S. thompsoni* because the two taxa differ only biometrically and, more important, both species have intermediate number of muscle fibres (CALDWELL, 1966; ESNAL, 1970).

FOXTON (1961) separated these two species on the basis of the following characters:

Solitary form	
Number of muscle fibres (M IV): 70–130 (mean 93.2)	
Ratio of body length/muscle width 21.2.....	<i>Salpa thompsoni</i>
Number of muscle fibres (M IV): 36–71 (mean 48.8)	
Ratio of body length/muscle width 35.8.....	<i>Salpa gerlachei</i>
Aggregate form	
Number of total muscle fibres: 140–235 (mean 177.7)	
Ratio of body length/muscle width 18.9.....	<i>Salpa thompsoni</i>
Number of total muscle fibres: 113–159 (mean 128.8)	
Ratio of body length/muscle width 27.6.....	<i>Salpa gerlachei</i>

The key characters presented above show that there is an overlap of 19 fibres (between 140 to 159) in the case of the aggregate form, suggesting that the separation between two species is not so clear. FOXTON (1961) did not include the original data and therefore it is not possible to check through a Significance Test the difference between the number of muscle fibres of both species. FOXTON also remarked that there is no north-south gradient in the number of muscle fibres over the distribution boundary separating these two species. Instead, he found a drastic change in the fibre numbers. Along the latitudinal transect at 90°W (Fig. 9) both species were collected (north of 65°S, *S. thompsoni*; south of 65°S, *S. gerlachei*). Our data showed no drastic change in the total number of muscle fibres of the aggregate form, but a gradual decrease of the same number south of 56°S (Fig. 6a). The ratios of body length/muscle width in eight different areas (see Table 2) almost coincided with those given by FOXTON for the solitary and aggregate forms of *S. thompsoni*. Since this ratio is constant for a given species, it is probable that these two species are a synonym.

According to the present results, it is impossible to distinguish *S. thompsoni* from *S. gerlachei*, especially in the specimens collected from the distribution boundary of the two species. Most animals have intermediate numbers of muscle fibres. Therefore, *S. gerlachei* is possibly an extreme case of the latitudinal variation of *S. thompsoni*.

5. Conclusions

S. thompsoni shows a latitudinal variation pattern in which the number of muscle

fibres as well as the body length decreases gradually from the north to the south in the Southern Ocean. On the contrary, the number of muscle fibres and the body length increase from the tropical water to the temperate waters, possibly because of the effect of low temperature. The variation of *S. thompsoni* probably represents an adaptation to the Antarctic waters especially for populations living at higher latitudes, where their growth rate varies and the summer swarming (budding) activity is restricted to a short period of time.

The gradual decrease in the number of muscle fibres from the north to the south as well as the wide overlap in the same number of *S. thompsoni* and *S. gerlachei* make it impossible to separate these two species. The ratio of body length/muscle width is rather constant from the north to the south, also suggesting to be a single species. Therefore, it is considered that *S. thompsoni* and *S. gerlachei* are synonymous species and that *S. thompsoni* shows a clinal variation along its north-south distribution.

It is still not clear if latitudinal variation in the number of muscle fibres represents a phenotypical adaptation to different environmental conditions or the populations living in latitudinally different areas have some genetical differences. The clinal variation would be attributed to the effect of sea water temperature and water density or current speed. A probable relationship between the current speeds and the fibre numbers was obtained in the present study. Seasonality of food abundance may be the important factor in the morphological (phenotypical or genotypical) differences of salps.

Acknowledgements

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