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ORIGINAL ARTICLE

Thalia longicauda (Quoy and Gaimard) from the south-western Atlantic Ocean (31°S–38°S): distribution and population structure

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Although the salp *Thalia longicauda* is common in the southern hemisphere, there is little information on its biology and ecology. Our study aimed to describe the morphology of the development of solitaries and aggregates and to determine the developmental stages, length distribution and population structure of this species. Plankton samples were collected by the R/V ARA “Puerto Deseado” from 31°55’S to 38°08’S (October 2013). *Thalia longicauda* was present at 50% of the stations, ranging between 1.21 and 2970 ind. 1000 m⁻³. Solitaries and aggregates represented 53.76 and 46.24%, respectively. We described the growth of the blastogenic stolon and the formation of blocks of aggregate buds. Each solitary may produce at least three blocks with a total of 36–86 aggregate buds. The relationship between total number of aggregate buds (y) and total length of the solitary (x) was $y = 3.321x - 13.489$. We characterized six developmental stages for solitaries and four for aggregates. The juvenile/mature ratio of solitaries and aggregates suggested that the population was actively reproducing both sexually and asexually. Based on seawater temperature and salinity data, *T. longicauda* may be considered as a temperate species inhabiting the southern range of subtropical waters and the northern range of sub-Antarctic waters.

KEYWORDS: maturity stages; Salpidae; *Thalia longicauda*; zooplankton

INTRODUCTION

Salps are marine gelatinous zooplankton usually found at low densities (e.g. Blackburn, 1979; Heron and Benham, 1984; Deibel and Paffenhof, 2009), but they are able to form dense swarms in oceans around the world.

Salps are efficient filter feeders (Madin and Deibel, 1998), which are capable of retaining particles between 2 μm and 1 mm (Vargas and Madin, 2004; Sutherland *et al.*, 2010) through their mucous net. Moreover, these individuals produce fecal pellets that contribute significantly to the vertical carbon flux to deeper waters (e.g. Caron *et al.*, 1989; Phillips *et al.*, 2009; Smith Jr. *et al.*, 2014).

The complex life cycle of salps alternates between the solitary asexual generation and the aggregate sexual generation. The solitary form produces a long stolon which, as it lengthens, becomes differentiated into blocks of aggregate buds that are released after they are fully developed.

Aggregates are protogynous hermaphrodites, and their ovary may contain from a single (in most species) to several ovarian sacs (OSs) (i.e. oocyte plus follicular cells) as in the case of *Ihlea magalhanica* (Daponte and Esnal, 1994) and *Iasis zonaria* (Daponte *et al.*, 2013). Once fertilized, the OS is retained within the ovary and develops into a solitary embryo (EMB) that remains attached to the maternal aggregate by a sort of placenta (PL). After the EMB is set free, the aggregate becomes to function as a male: its testes mature, releasing the sperm that fertilize the ova of the new aggregates (Miller and Cosson, 1997).

The young solitary develops and the stolon grows in length, forming aggregates by budding. According to the species, the stolon may produce aggregate buds continuously, which are released as they are fully developed without block formation (Esnal and Daponte, 1990), or may develop a series of chains (blocks) of aggregate buds which are released one at a time (Heron and Benham, 1985).

The distribution of salps is largely determined by sea-surface water temperature and food availability (Van Soest, 1975; Henschke *et al.*, 2015). Their horizontal distribution is influenced by different marine currents around the world, which are characterized by distinctive ranges of temperature, salinity, dissolved oxygen and nutrients. So, salp species reproduce and grow under favorable environmental conditions in the water mass they inhabit (e.g. Deibel and Lowen, 2012; Henschke *et al.*, 2015). Indeed, under optimal conditions, they can form dense swarms over large areas of the world's oceans with asexual reproduction being regarded as the main driver of salp swarming.

High densities of salps can affect ecosystem functioning mainly by altering the epipelagic food web

(Landry and Calbet, 2004), increasing the export flux of organic matter to the deep layers (e.g. Fortier *et al.*, 1994) and decreasing the organic matter available to other trophic levels (e.g. Dubischar and Bathmann, 1997).

So far, salp blooms have been reported for some species of a few genera such as *Salpa* (*Salpa aspera*, *Salpa thompsoni*, *Salpa fusiformis* and *Salpa maxima*), *Thalia* (*Thalia democratica*), *Cyclosalpa* (*Cyclosalpa bakeri*), *Iasis* (*I. zonaria*), *Ihlea* (*Ihlea magalhanica* and *Ihlea racovitzai*) and *Thetys* (*Thetys vagina*) (e.g. Wiebe *et al.*, 1979; Bathmann, 1998; Perissinotto and Pakhomov, 1998; Iguchi and Kidokoro, 2006; Madin *et al.*, 2006; Daponte *et al.*, 2011; Pakhomov *et al.*, 2011; Loeb and Santora, 2012; Giesecke *et al.*, 2014). Indeed, there is very scarce information on swarms produced by other species.

The impact of the salps bloom over the ecosystem emphasizes the need to determine which species are capable of producing swarms and to gain a better understanding of the reproductive mechanisms underlying swarming.

Among salp species known to form swarms, *T. democratica* has been extensively studied, in particular, with regard to reproductive and ecological aspects (e.g. Heron, 1972; Deibel, 1982; Heron and Benham, 1985; Licandro *et al.*, 2006; Henschke *et al.*, 2011, 2014). However, there is little information on other species of the genus, such as *Thalia longicauda*, a typical species of the southern hemisphere. It was described in 1824 by Quoy and Gaimard (Quoy and Gaimard, 1824) based on the individuals collected near Port Jackson (East Australia) and was then fully re-described by Godeaux (1967), who confirmed that *T. longicauda* clearly differs morphologically from the other species of the genus *Thalia* (Van Soest, 1973). Its presence has been reported by several authors (e.g. Apstein, 1906; Krüger, 1939; Amor, 1966; Esnal, 1970), but still, many aspects of its basic biology and ecology remain unknown.

To contribute to the knowledge of *T. longicauda*, our aims were to (i) analyze the morphology of the development of the OS and stolon, (ii) estimate the number of blocks and buds produced by the stolon as an indicator of sexual reproduction and (iii) determine developmental stages for aggregates and solitaries to analyze its population structure in an area of the south-western Atlantic Ocean.

METHOD

Study area

The studied area (Fig. 1A) corresponds to a sector of the south-western Atlantic Ocean where two boundary currents, the Brazil Current (BC, a southward branch of

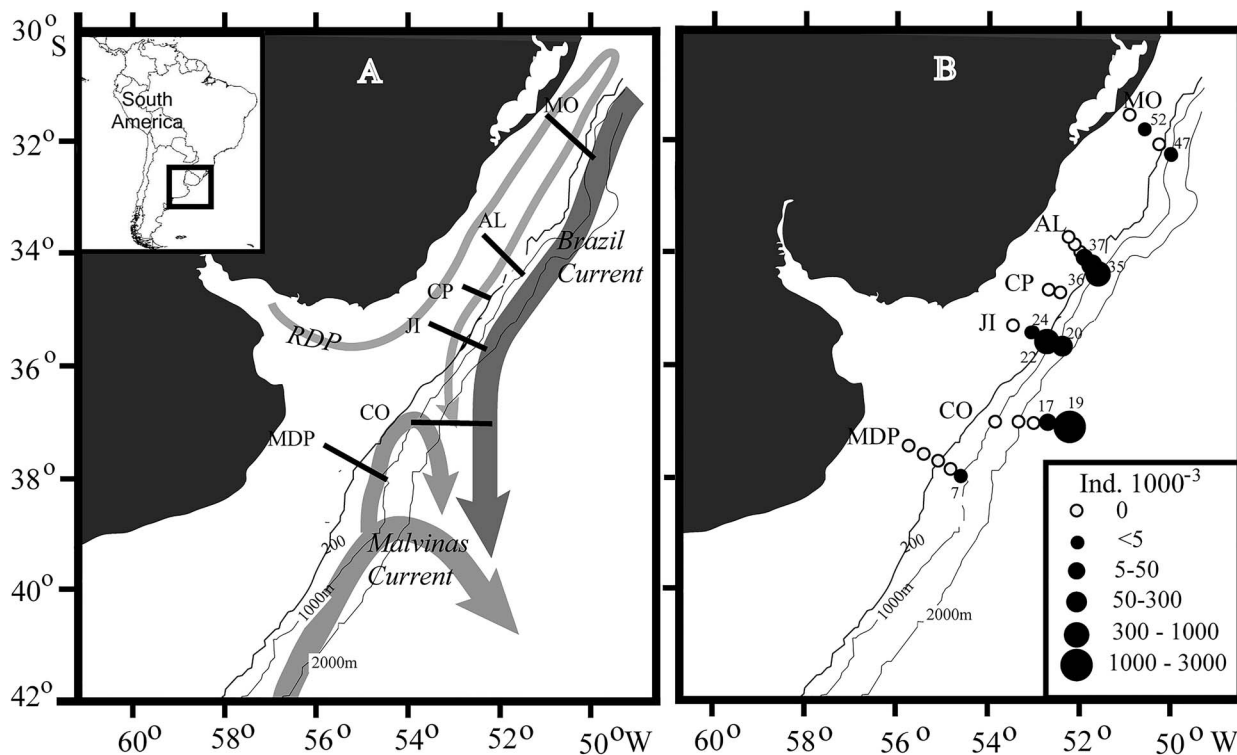


Fig. 1. (A) Location of sampling transects at the studied area of the south-western Atlantic Ocean and schematic representation of the oceanic circulation (light gray lines). (B) Position of sampling stations and abundance (expressed as individuals 1000 m^{-3}) of *T. longicauda*.

the Atlantic South Equatorial Current) and the Malvinas Current (MC, a northward branch of the Antarctic Circumpolar Current), converge and flow offshore originating the Brazil-Malvinas Confluence (around 38°S ; Gordon and Greengrove, 1986; Palma *et al.*, 2008). The interaction between these two currents generates eddies and meanders, with thermal and haline characteristics differing from those of the surrounding waters.

The BC flows in a southerly direction along the shelf break (Fig. 1A) carrying two water masses, Tropical Waters (TW; Palma *et al.*, 2008) at the surface and South Atlantic Central Waters (SACW; Thomsen, 1962) below the surface (at depths between 100 and 600 m).

The MC (Fig. 1A), which flows northward following the shelf break of the Argentine shelf advects sub-Antarctic Waters (SAW; Thomsen, 1962) at the surface and Atlantic Intermediate Water (AAIW; Tomczak and Godfrey, 1994) below. The MC is divided into the eastern and western branches. The western branch carries sub-Antarctic Shelf Waters (SASW; Piola *et al.*, 2000) northward over the continental shelf, mixing all along the way with freshwater discharges from rivers. The SASW reaches 33°S and returns southward after splitting into two branches (Berden *et al.*, 2020) and meets a south-westward flow of subtropical Shelf Waters (modified TW/SACW diluted

by continental runoff from the coast; Piola *et al.*, 2000), creating the subtropical Shelf Front (STSF; Piola *et al.*, 2000).

In addition, a superficial low-salinity tongue of Rio de La Plata (RDP, Fig. 1A) waters extends northward over the STSF up to 32°S (Berden *et al.*, 2020) and offshore; filaments of low-salinity surface waters have been identified in open ocean waters (Guerrero *et al.*, 2014).

Finally, near the bottom in the outer shelf between 32°S and 35°S , an intrusion of SACW mixes with shelf waters and is ultimately exported offshore through the Brazil-Malvinas Confluence (Berden *et al.*, 2020).

Sampling

Plankton samples were collected by the R/V ARA “Puerto Deseado” from the south-western Atlantic Ocean ($31^{\circ}55'\text{S}$ – $38^{\circ}08'\text{S}$) in early spring (3–10 October 2013).

Samples were taken along six transects (Fig. 1A and B) perpendicular to the coastline: Mostardas (MO, $31^{\circ}55'\text{S}$), Albardao (AL, $34^{\circ}50'\text{S}$), Cabo Polonio (CP, $34^{\circ}65'\text{S}$), José Ignacio (JI, $35^{\circ}68'\text{S}$), Confluencia (CO, $37^{\circ}05'\text{S}$) and Mar del Plata (MdP, $37^{\circ}33'\text{S}$). Sampling was conducted from coastal waters (55 m depth) to open ocean

using a Rectangular Midwater Trawl net modified from Baker *et al.* (1973) with a mouth opening of 1 m² and mesh size of 500 µm. The net was towed obliquely from just above the bottom to the surface in shallow waters and from 200 m depth to surface beyond the continental slope.

The filtered volume was determined with a digital flowmeter. Samples were preserved in 2% buffered formaldehyde in seawater.

Temperature and salinity were measured with a CTD (Seabird Electronics 911 Plus) from near bottom to the surface at shelf stations and from 600 to 1000 m deep to the surface at most oceanic stations.

Sea-surface chlorophyll *a* concentrations were obtained from monthly composite satellite images of the study area, which were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard Aqua (EOS PM) satellite. MODIS data were provided by NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, USA (<http://oceancolor.gsfc.nasa.gov>) (NASA, 2019).

Laboratory procedure

For each sample, all the solitary and aggregate individuals of *T. longicauda* were sorted out, counted and measured. Salp abundance was expressed as number of individuals per 1000 m³. A one-fourth subsample was taken from samples >2000 individuals. Total length (TL) of aggregates and solitaries was measured from the oral opening to the posterior ridge of the gut, exclusive of the outer test (Foxton, 1966). Length–frequency distributions were based on the number of measured individuals and 1-mm length intervals.

The developmental morphology of the stolon and ovary was considered in well-preserved solitaries and aggregates. The morphology of the ovary and stolon of each individual was observed under a stereomicroscope and a microscope, and those measurements were taken with a graduated eyepiece. Rose bengal was used when necessary and figures were drawn with the aid of a camera lucida.

We considered the following external features observed during the progressive growth of the stolon: stolon position with respect to the digestive loop (DL), number of blocks (group of aggregates of the same size and age), number of aggregate buds per block in fully developed blocks, presence of a scar in the tunic and presence of a region of abortive buds (intermediate piece (IP)) between successive blocks. Since each block is composed of a double row of buds, the total number of buds per block was obtained by doubling the number of buds in one row. Blocks were considered to be fully developed only if they could be clearly distinguished from the stolon, thus

reducing the possibility of including young chains (still undergoing segmentation) in the analysis (Henschke *et al.*, 2014).

For free aggregates, we considered the morphology of the OS, size of the developing EMB, presence of EMBs >9 mm, presence of placental remnants corresponding to the Foxton's "spent" stage (Foxton, 1966) or of a placental scar resulting from placental detachment after EMB release.

All these traits were used to establish developmental stages for the solitaries and aggregates of *T. longicauda*. The criteria used to define the developmental stages were modified from those described by Heron and Benham (Heron and Benham, 1985) for *T. democratica*. In addition, developmental stages were grouped into juvenile (solitaries: Stages I–III; aggregates: Stages UD–DE) and mature individuals (solitaries: Stages IV and V; aggregates: Stages FD–SP). Due to the scarce information on the biology of *T. longicauda*, we considered that solitaries were mature when they showed two fully developed blocks or one fully developed block and a scar in the tunic. Likewise, aggregates were considered to be mature if they had a fully developed solitary (>10 mm) or a placental scar.

To characterize the studied population of *T. longicauda*, we determined the following life history parameters, which are modified from those proposed by Heron and Benham (1985) for the phylogenetically related *T. democratica*:

- A: Number of blocks produced by solitaries;
- B: number of buds at the distal block (DB) in solitaries (used as an indicator of asexual reproduction, Henschke *et al.*, 2014);
- C: length of the most abundant mature stage in solitaries;
- D: relationship between the number of mature and juvenile stages of the solitary generation (Heron and Benham, 1985);
- E: ratio of juvenile to mature aggregates;
- F: percentage of undeveloped aggregates and
- G: aggregate to solitary ratio, considering all stages of the aggregate generation (Juvenile, UD - Spent, SP) and all stages of the solitary generation (I–V).

Data analyses

The Spearman rank order correlation test was used to examine the spatial correlation of *T. longicauda* abundance and water chlorophyll-*a*, since this non-parametric method is suitable for the analysis of data that are not distributed normally.

A regular (Model I) regression analysis was carried out to determine the relationship between the total number of buds and TL of *T. longicauda*. The significance

of the regression was tested by analysis of variance (ANOVA) and the proportion of the variance in the number of buds explained by TL was calculated by the coefficient of determination (R^2). Finally, length–frequency distributions of the developmental stages were compared separately for the solitary and aggregate generations at stations with higher abundances (i.e. stations 17, 19, 22 and 35, Fig. 1B) using two-factor (developmental stage and station), fixed-effect ANOVA. Body length values were not normally distributed, so they were rank-transformed and analysis was performed using the two-way ANOVA on ranks approach recommended by Conover (Conover, 1999). Tukey-type multiple comparison test for unequal sample size was used for *post hoc* comparisons after ANOVA on ranks (Zar, 1999).

RESULTS

During October 2013, we detected the following five water masses in the study area from 0 to 200 m depth, which was in agreement with Berden *et al.* (Berden *et al.*, 2020): (i) The SASW in the southern portion of the shelf (salinity: 33.6–33.8, $T < 11^\circ\text{C}$); (ii) the RDP water on the continental shelf, north-east of the MDP transect, extending north of the estuary as a buoyant layer over other water masses (salinity < 32 , $T > 10^\circ\text{C}$); (iii) TW found offshore (salinity > 35 and $T > 19^\circ\text{C}$); (iv) SACW on the outer shelf at transects JI, CP and AI (salinity > 34.5 , $T < 19^\circ\text{C}$) and (v) Antarctic Intermediate Water (AAIW) in the offshore region of transects CO, AL, CP and JI, mixed with other water masses (salinity: 33.5, T : 3.4°C). The water masses show a different degree of mixing where they overlap with other water masses. The STSF was detected at transect JI between stations 23 and 21 and at transect AL between stations 36 and 37. Although sea-surface chlorophyll-*a* concentrations were based on monthly composite satellite images, higher abundances of *T. longicauda* were mainly related to lower chlorophyll-*a* concentrations (except for station 37; Fig. S1, see online supplementary data for a color version of this figure), but the negative correlation was not significant ($r_s = -0.34$; $P = 0.12$).

Thalia longicauda was found at 50% of the sampling stations at five of six transects. It was absent at the inner and middle shelf stations. The abundances at stations located from the shelf break to the open ocean ranged from 1.21 to 2979 ind. 1000 m^{-3} (Fig. 1B). Only stations with > 100 ind. 1000 m^{-3} were considered for the population analysis of *T. longicauda* (stations 17, 19, 22 and 35); the environmental characterization of these stations is shown in Fig. 2 (temperature, salinity and water masses) and in Fig. S1, see online supplementary data for a color

version of this figure (surface chlorophyll-*a* with values $< 0.80\text{ mg m}^{-3}$).

Development of aggregates and solitaries

Aggregates: development of the EMB

The ovary lies dorsally at the wall of the atrial cavity and contains a single ovum surrounded by follicular cells, constituting the OS. When the OS shows no sign of fertilization, it is round in shape and usually does not exceed 0.4–0.5 mm in diameter. After fertilization, the EMB is nourished by the PL. When the EMB is < 0.9 mm, the internal structures become noticeable, the PL increases in size and the eleoblast (EL, transient hematopoietic gland) undergoes development.

The muscles, endostyle, dorsal ganglion, EL and the transparent gut can be clearly distinguished in the fully mature EMB which is still attached to the parent (Fig. 3A) with a size between 1 and 2.5 mm. At this stage, the PL reaches its maximum size and the outline of the stolon is visible ventrally. Once the mature EMB was released, the base of the PL remains attached to the aggregate (spent individuals).

Solitaries: development of the stolon

The newly born solitaries exhibit remains of embryonic tissues (EL and PL), which become reduced as development proceeds (Fig. 3B and C). The stolon, which is placed in the mid-ventral region between the anterior part of the DL and the posterior end of the endostyle, grows around the DL, while blocks of buds continue their development. As the stolon elongates, it digs a tunnel in the tunic through which it emerges.

The strobilation of the stolon begins in the growing zone (GZ, Fig. 3D), which is located at the stolon's proximal end. At first, the segments or buds are aligned in a single row (Fig. 3D), and later, they become rearranged into a double row at the deployment point (DP, Fig. 3E). The developing aggregates increase gradually in length from the proximal to the distal end of the stolon (Fig. 3E). The stolon grows around the DL, while the buds continue development and differentiation, with its DL being the last structure to be clearly distinguished. In mature solitaries, the stolon shows two blocks of buds of different length, namely, the proximal block (PB, the new one) and DB (the older one), and forms a spiral which completely surrounds the DL (Fig. 3F), with its tip being in the anterior sector of the DL. The DB is the first to be released into the ocean through a tunnel opened ventrally (in the anterior sector of the DL) after which the opening is closed leaving a scar. The next block is released through the opening at the scar site. Both blocks of fully developed

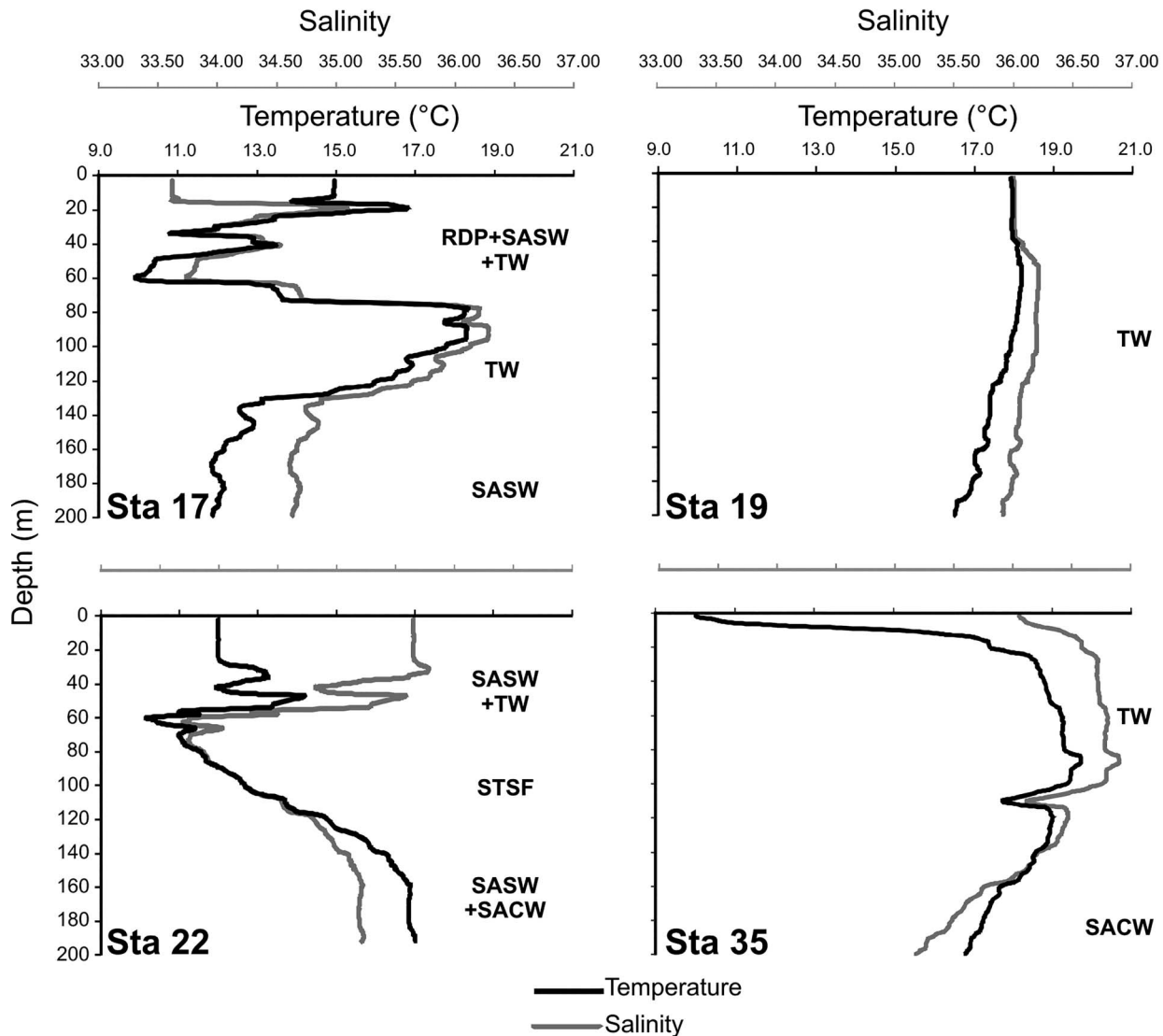


Fig. 2. Vertical profiles of temperature (black line) and salinity (gray line) through 200 m at Stations 17, 19, 22 and 35.

aggregates reach different lengths before they are set free (Fig. 3F), with the mean length of the aggregates in the DB (>1.5 mm) being higher than that of the PB. The free-living aggregates begin to feed and their DL turns darker.

The fully developed stolon (Fig. 3F) presents two blocks of aggregates (buds), which appear from the DP. No abortive buds forming an “IP” was observed between the PB and DB.

The total number of aggregate buds in the stolon was positively correlated with the TL of the solitary, described by $y = 3.321x - 13.489$, where y is the total number of aggregate buds per solitary and x is the TL of the solitary ($R^2 = 0.816$; $n = 99$) (Fig. 4).

In specimens with fully developed blocks, the number of buds in the stolon ranged from 26 to 86 (mean + standard deviation (SD) = $54.91 + 10.47$). The number of buds was lower in the PB than in the DB in >35% of solitaries, and both blocks had the same number of buds in >19% of solitaries, while the PB had only a few more aggregates than the DB in the remaining individuals.

Developmental stages of *T. longicauda*

Aggregates

Individuals were classified into four stages based on the gradual growth of the EMB within the aggregate parent

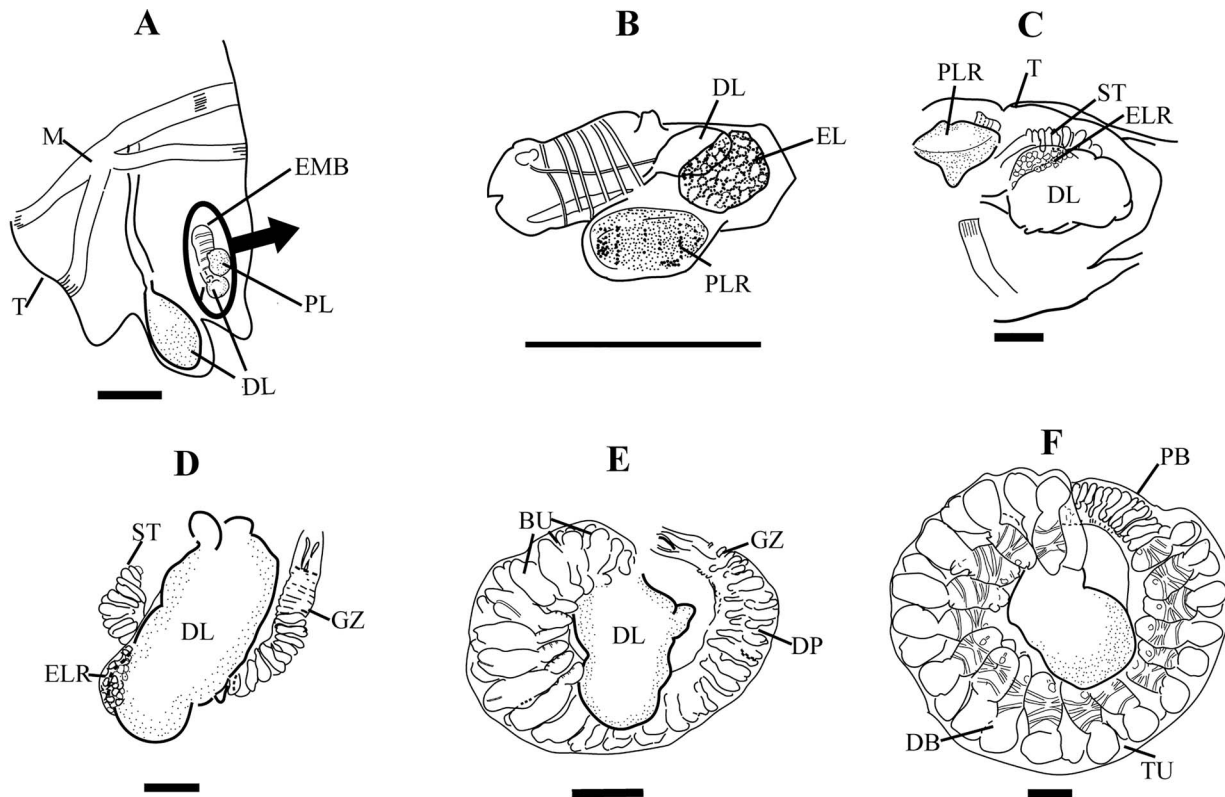


Fig. 3. Developmental stages of *T. longicauda*. (A) Posterior part of an aggregate with a mature EMB. (B) Recently released young solitary. (C) Juvenile solitary with stolon starting to form and reduced embryonic tissues. (D) Growing stolon with aggregate buds in a single row. (E) Stolon forming a DB of aggregate buds. (F) Fully developed stolon with two blocks of aggregates (DB and PB). BU: buds of aggregates, M: muscle, ELR: EL remains, PLR: placental remains, ST: stolon, T: tunic, TU: tunnel (through which the stolon elongates). Scales: A: 0.8 mm; B: 1 mm; C–F: 0.4 mm.

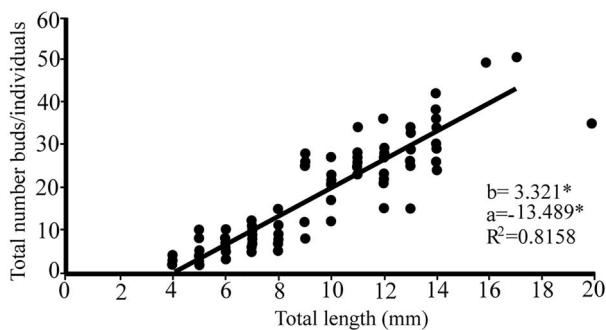


Fig. 4. Production of aggregate buds as a function of TL of the solitary of *T. longicauda*. Estimated values of the regression parameters are shown. a: y intercept; b: slope; R^2 : coefficient of determination. *Significance at probability level of 0.05.

and the presence of placental remnants or a placental mark indicating the release of the EMB (new solitary), as follows:

UD: juvenile, without evidence of oocyte development, ovary spherical (0.4–0.5 mm);

DE: developing oocyte, elongated (0.5–0.9 mm), showing different degrees of development but lacking clearly identified internal structures (<0.9 mm);

FD: EMB (>1 mm), which is still attached to the aggregate by the PL and showing fully developed internal organs; this is the first mature stage and

SP: spent, placental scar visible on the dorsal side of the tunic;

During the study period, stage UD was the most abundant, followed by stages DE, FD and SP, which showed different frequencies according to the sampling station.

At all the stations, the length of the aggregates increased linearly from stages UD to SP, but stages FD and SP were almost of the same size (Fig. 5).

Solitaries

EMB: EMB freed from its aggregate parent, with a large PL and EL (embryonic tissues) and transparent intestine (empty gut).

I: Young stage with reduced PL and EL; dark intestine (containing food); stolon with few segments located

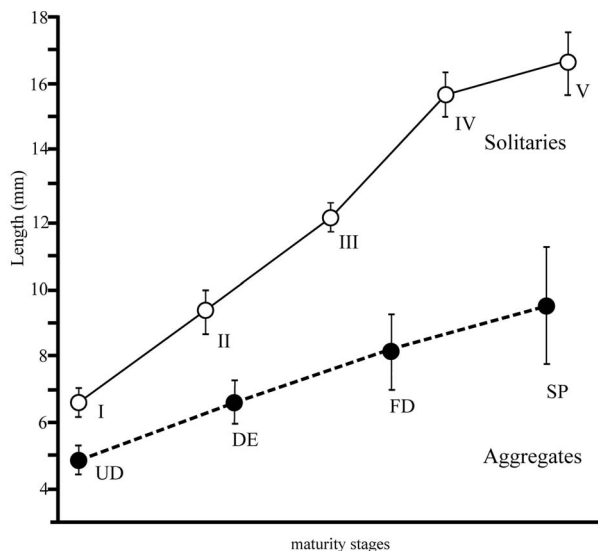


Fig. 5. Growth curve: TL (mean + SD) of maturity stages of *T. longicauda* aggregates (UD, DE, FD and SP) and solitaries (I–V).

in a single row, reaching approximately one-fourth turn around the DL.

II: Young stage with no placental remains or EL; segmented stolon reaching half way around the DL; most buds located in a single row, some aggregate buds placed in a double row at the distal end of the stolon.

III: Stolon with a completely differentiated block of aggregate buds (DB) and a second block undergoing segmentation. Stolon reaches more than three-fourths of a circle around the DL. Aggregates of the DB are of the same length.

IV: Two fully differentiated blocks and a third block undergoing segmentation; scar absent. This is the first mature solitary stage.

V: One or two blocks; scar present, indicating the release of at least one block of aggregates.

Solitaries in Stage III were the most abundant followed by Stages I, IV, II, EMB and V. The length of the solitaries

increased from Stages I to V, but Stage IV was slightly shorter than Stage V (Fig. 5).

Length distribution of developmental stages

Aggregates showed no significant differences in the TL of each developmental stage among sampling stations (ANOVA: $F_{9, 721} = 0.47$ $P = 0.89$). By contrast, solitaries showed significant differences (ANOVA: $F_{11, 352} = 5.31$, $P = 0.000$); the TL of stages IV and V at Stations 22 and 35 was significantly lower than at Stations 17 and 19 (Tukey’s test, $P < 0.02$), while the TL of Stage I was higher at Station 22 than at Stations 19 and 17 (Tukey’s test, $P < 0.01$).

In the sampling area, the frequency of solitaries (53.76%) was higher than that of aggregates (46.24%), but this relationship varied according to the stations. It was higher at Station 19, lower at Stations 17 and 22 and similar at Station 35 (Table I). At all the stations, both generations (aggregates and solitaries) were recorded at all maturity stages. The juvenile aggregates (Stages UD and DE) showed higher frequencies than did matures (Table II; Fig. 6). Similar results were observed for solitaries with juvenile stages (I–III) being more frequent than matures (Table III; Fig. 6).

EMBs were only found at Stations 17 and 19 (Table III) at very low frequencies, probably due to the mesh size of the net.

When considering the entire sampling area, the mean TL of free aggregates ranges between 3 and 10 mm (Fig. 6A, C, E and G) and that of aggregates with placental scar or placental remnants between 9 and 10 mm. The mean size (\pm SD) sizes of the aggregates were: UD: 5.65 (\pm 1.27), SD: 7.34 (\pm 1.03), FD: 8.42 (\pm 1.06) and SC: 9.63 (\pm 0.50). Table II shows the TL for each stage at each station. It is worthy of note that mean TL values of stages UD, DE and FD were somewhat higher at Station 17 than at the other stations (Table II).

Table I: Life history parameters of T. longicauda at each station (Sta) at the survey area; Mean + (SD)

	Sta 17	Sta 19	Sta 22	Sta 35
Solitaries percent contribution (%)	11.60	75.86	42.63	50.37
Aggregate percent contribution (%)	88.39	24.14	57.36	49.62
A. Number of blocks produced (solitaries)	1.86 (0.69)	1.12 (0.33)	1.73 (0.59)	1.25 (0.55)
B. Average number buds at DB (solitaries)	27.77 (7.71)	18.23 (9.67)	31.43 (6.74)	23.71 (3.87)
C. Length of the most abundant mature stage (IV—solitaries)	15.0 (1)	15.6 (2.61)	13.24 (1.45)	12.00 (0.71)
D. Relationship mat. and juvenile in the sol.	0.85	0.27	0.53	0.64
Generation = $ABS\{1 - [(IV - V)/(I - III)]\}$				
E. Juvenile to mature ratio (aggregates)	12.33	7.0	12.0	17.1
F. Percentage of undeveloped (aggregates)	77.5	62.5	81.66	90.05
G. Aggregate/solitary ratio (va)	8.5	0.14	1.34	0.98

Table II: *Thalia longicauda* percent of occurrence of aggregate maturity stages for each station (Sta); TL in mm.

	Sta 17	Sta 19	Sta 22	Sta 35
UD—occurrence (%)	77.50	62.50	81.65	90.06
TL: mean (SD)	6.69 (0.76)	4.89 (0.87)	5.39 (1.32)	5.60 (1.66)
DE—occurrence (%)	15.00	25.00	10.65	4.97
TL: mean (SD)	8.0 (0.51)	6.64 (2.10)	6.83 (1.16)	7.33 (0.50)
FD—Occurrence o(%)	3.75	8.93	6.80	3.31
TL: mean (SD)	9.5 (0.55)	8.2 (0.45)	8.25 (1.11)	8.71 (0.95)
SC—occurrence (%)	3.75	3.57	0.89	1.66
TL: mean (SD)	9.67 (0.52)	9.50 (0.71)	9.33 (0.58)	9.5 (0.58)

When considering all the stations, the mean TL distribution of solitaries ranged from 4 to 20 mm (Fig. 6B, D, F and H) the mean (\pm SD) length of each stage was: I: 7.45 (\pm 1.48), II: 9.11 (\pm 1.59), III: 12.30 (\pm 1.28), IV: 13.51 (\pm 1.36) and V: 15.21 (\pm 2.09). Table III shows the mean TL for each stage at each station. The values of mature Stages IV and V were higher at Station 19 than at the other three stations analyzed; these stages were probably responsible for the high abundance of the stage UD of the aggregate generation (Table II, Fig. 6D). At Station 35, Stages III and IV exhibited the lowest mean TL values compared with the other stations, which resulted in non-significant differences in TL between advanced juveniles and matures (Table III). Finally, the frequency of mature solitaries was higher at Station 22 than the other stations.

Table I shows data on life history parameters for the *T. longicauda* population in the survey area.

Although at Station 36, *T. longicauda* showed an intermediate abundance (306 ind.1000 m⁻³), we could only determine the aggregate to solitary ratio (0.87) due to the poorly preserved condition of the individuals.

It is important to note that at stations with low abundance of individuals (i.e. 20, 24, 37, 47 and 52), solitaries were more abundant than aggregates, with the aggregate to solitary ratio ranging between 0.5 and 0.8.

DISCUSSION

This is the first study focused on the development of solitaries and aggregates and on the population structure of *T. longicauda* from the south-western Atlantic Ocean.

Abundance and horizontal distribution

Our results showed that the abundance of *T. longicauda* increased from the shelf break to the open ocean. The low values of chlorophyll-*a* may explain the usually low abundance of salps in oceanic areas. Most of salp species are indiscriminate filter feeders which are unable to regulate their filtration rate, and a high concentration of

suspended particles leads to the clogging of the food-trapping mucous net (Harbison and Gilmer, 1976). Internal and middle shelf areas often contain a high density of suspended particles which will disrupt the feeding mechanism (Deibel, 1982; Harbison *et al.*, 1986), thus preventing most of these species from inhabiting coastal environments. This, together with the lower salinity of RDP waters (<32.00) are likely to account for the absence of *T. longicauda* at stations on the internal and middle shelves.

High abundance of *T. longicauda* was mostly found at stations in which warmer waters predominates. Station 19 showed TW through the entire water column related to a warm detachment of the BMC (Berden *et al.*, 2020), and the remaining stations showed warm waters on the surface and cooler waters beneath (SACW or SACW mixed with SASW, Fig. 2). At these stations, SST and salinity values were similar to the historical data. Previous information showed that at the South Atlantic Ocean the highest abundance of *T. longicauda* was recorded by Apstein (1906) in the western sector of the Benguela Current at stations with SST between 16.1 and 16.5°C during the Deutschen Tiefsee-Expedition, while Krüger (1939) reported its presence at 16.8 (February) and 12.3°C (September) during the Meteor Expedition. It was found among 14.6 and 18.2°C at 42° 55'–43° 43'S by Amor (1966) and from 11.7 to 17.5°C (36° 30'–38° 00'S) by Esnal (1970). In addition, *T. longicauda* was not found in warmer waters; it was neither found north of 30° S in the SWAO (Esnal and Daponte, 1999) nor in warmer waters of the Pacific Ocean (Yount, 1958) or the Pacific Ocean (Yount, 1958) or the Philippine Archipelago (Metcalf, 1918).

Taken together, our results and the above historical data suggest that *T. longicauda* from the SWAO may occur in the subtropical waters located further south (i.e. cooler) and SAW located further north (i.e. warmer).

Development

The embryonic development of *T. longicauda* seems to be similar to that described for other salp species

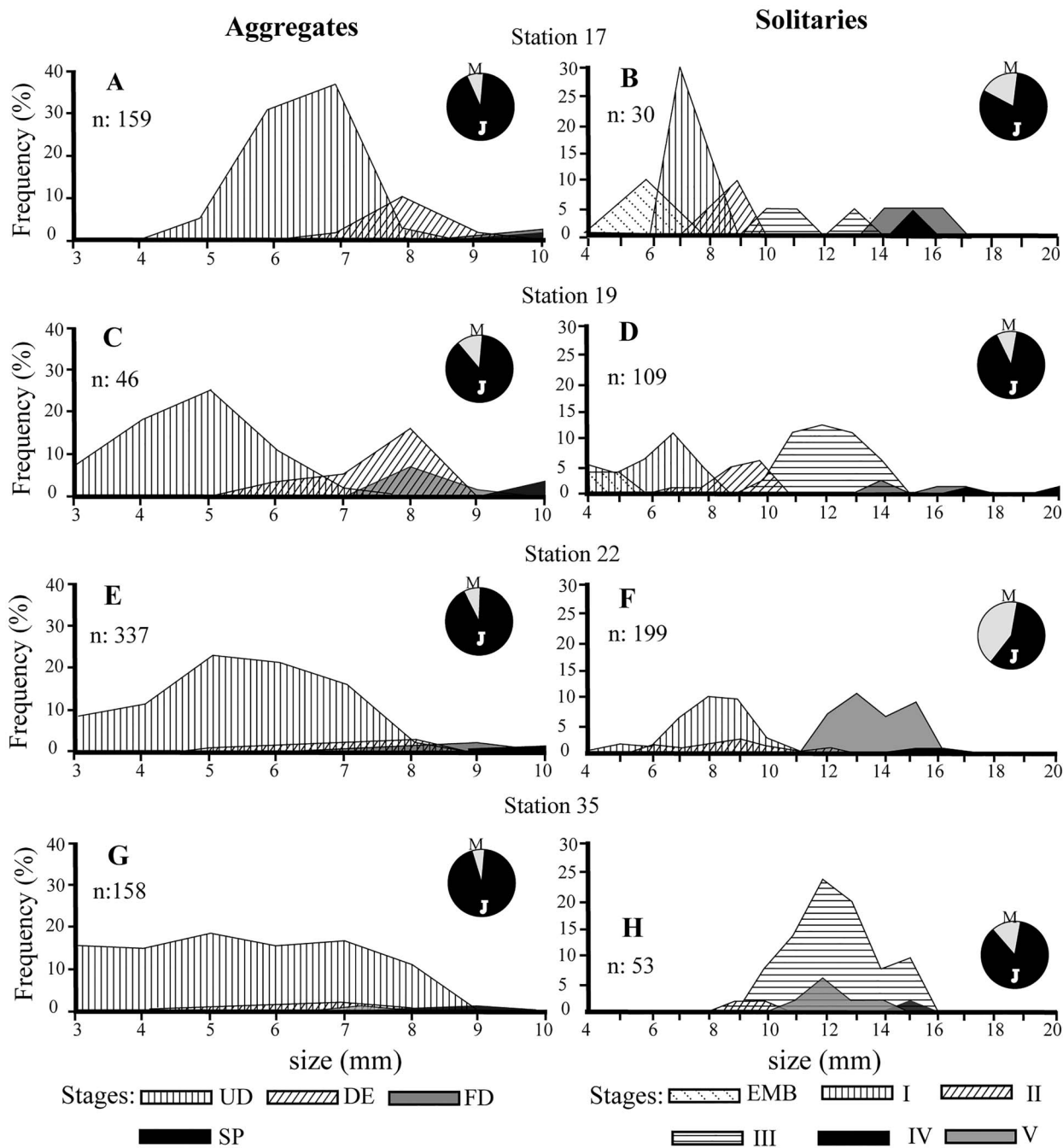


Fig. 6. Length-frequency distribution of maturity stages of *T. longicauda* solitaries and aggregates per station. Pie charts indicate the proportion of juvenile and mature stages for solitaries and aggregates per studied station. *n*: total number of individuals. Solitaries (A: sta. 17; C: sta. 19; E: sta. 22 and G: sta. 35) and aggregates (B: sta. 17; D: sta. 19; F: sta. 22 and H: sta. 35).

(i.e. Brien, 1928) in which the ovary has only one OS and therefore will develop a single EMB. Once this EMB is released, the young solitary undergoes growth and development, while the embryonic tissues (PL and EL) gradually disappear and the stolon becomes longer.

Although the arrangement during the stolon development of *T. longicauda* resembles that of salp species producing successive linear blocks, it differs in some aspects. In *T. longicauda*, the stolon lacks the IP between blocks as observed in *I. zonaria* (Daponte *et al.*, 2013) and *S. thompsoni* (Foxton, 1966). Its scar in the tunic (left after the first

Table III: *Thalia longicauda* percent of occurrence of solitary maturity stages for each station (Sta); TL in mm.

	Sta 17	Sta 19	Sta 22	Sta 35
EMB—occurrence (%)	4.76	7.22		
I—occurrence (%)	42.86	30.12	31.66	
TL: mean (SD)	6.38 (0.48)	6.58 (1.08)	7.98 (1.33)	
II—occurrence (%)	14.29	13.25	10.05	3.92
TL: mean (SD)	8.83 (0.29)	9.18 (0.98)	8.87 (1.89)	9.5 (0.71)
III—occurrence (%)	19.05	42.16	16.58	82.35
TL: mean (SD)	12.66 (0.57)	12.31 (1.21)	12.80 (0.93)	12.37 (1.41)
IV—occurrence (%)	9.52	6.02	33.67	11.76
TL: mean (SD)	15.0 (1)	15.6 (2.61)	13.24 (1.45)	12.00 (0.71)
V—occurrence (%)	9.52	1.21	8.04	1.96
TL: mean (SD)	15.5 (0.71)	17	14.25 (1.34)	14.67 (0.58)

block was released) is located in the mid-ventral region and anterior to the DL, while it is posterior to the DL in the remaining *Thalia* species (Daponte *et al.*, 1996). In other species, the position of the scar varies with respect to the DL, as in *I. zonaria* (Daponte *et al.*, 2013) and *S. thompsoni* (Foxton, 1966). Other differences are related to the number of blocks and of aggregate buds per block. The asexual reproduction by solitaries involving the production of many offspring through stolon budding may be responsible for rapid population increases (Braconnot, 1963; Deibel, 1982) due to the large number of blocks and of buds per block.

We found individuals with two fully developed blocks of aggregate buds and a scar, suggesting that *T. longicauda* could produce at least three blocks with the potential to generate 36–86 aggregates. Such fecundity rate of solitaries is lower than that recorded for other species; Madin and Purcell (1992) reported that solitaries of *C. bakeri* produce ~170 aggregates over its lifespan, while *I. zonaria* could originate 480 aggregates, and these values decrease at lower temperatures (Daponte *et al.*, 2013). *Salpa thompsoni* gives rise to ~800 aggregates (Foxton, 1966; Casareto and Nemoto, 1986; Daponte *et al.*, 2001). In turn, the fecundity rate of solitaries of *T. longicauda* is similar to those of *T. democratica* (range: 32–112; Braconnot, 1963) and *Thalia sibogae* (Daponte *et al.*, 1996).

In salp species, each solitary during its lifespan may produce several blocks of aggregates, which realized different number of aggregates. The number of blocks and aggregates per block depend on solitary size and generation time, both of which are affected by latitudinal and seasonal differences in temperature and food availability (Foxton, 1966; Heron, 1972; Heron and Benham, 1985; Deibel and Lowen, 2012). Usually, smaller salps and short generation time (as *T. democratica*) produce lowest number of aggregates than larger species with longer generation time (as *S. thompsoni* or *C. bakeri*).

Population structure

Thalia longicauda showed a high abundance, with solitaries being more frequent (53.76%) than aggregates. This resulted in a low aggregate/solitary ratio (Table II) in contrast to those reported for blooms of other salp species. In a swarm of *T. democratica*, solitaries represented only 9–20% of the population (Henschke *et al.*, 2011), while the aggregate/solitary ratio in swarms of *S. thompsoni* ranged from 0.7 to 137 (Pakhomov *et al.*, 2006) or was up to 855.69 (Henschke *et al.*, 2018) in different areas of the Southern Ocean.

Although we found that aggregates were in a lower proportion than those reported for other species, the asexual reproduction of solitaries is necessary to increase the population size. Mature solitaries (Stages IV and V) were responsible for the high number of juvenile aggregates. The higher abundance of solitaries with one fully developed block and another one under development (juvenile Stage III) suggests that the number of mature Stages IV and V may increase in the short time, followed by a raise in the number of free aggregates.

We observed a high abundance of juvenile aggregates (UD, DE) in most of the stations, suggesting a recent release of blocks by mature solitaries.

The UD aggregates (females), which were present at higher frequencies, were going to be fertilized by the sperm of aggregates that had already released their EMBs (SP). Mature aggregates (FD–SP) were responsible for the large number of young solitaries (UD) found at all stations. The individuals of Stage V were most likely to die after shedding the sperm, thus reducing their frequency in the study area.

The juvenile/mature ratios of solitaries and aggregates may indicate that the analyzed population is actively reproducing both sexually and asexually. Moreover, the fact that the number of buds was lower in the PB (younger) than in the DB (older), suggests an accelerated

population growth rate (Heron and Benham, 1985), which is probably caused by the better environmental conditions (Deibel and Lowen, 2012) that are usually found in upwelling and frontal areas, as in the case of the STSF. High concentrations of phyto- and zooplankton, including salps, doliolids and appendicularians, have been reported from these areas (e.g. Deibel, 1982; Mianzan and Guerrero, 2000).

The presence of EMBs and the smaller size of EMBs and Stage I solitaries at the southern stations (17, 19; Fig. 6) suggest that the production and growth of young solitaries at these stations were delayed with respect to the northern stations, where EMBs and Stage I solitaries were scarce or absent (e.g. Station 35). The absence of these stages probably represents a sampling of an older patch of the population.

The fact that the size of mature solitary Stages (IV and V) was smaller at northern than at southern stations (under the influence of cooler waters) is in agreement with the general observation that maturity is reached earlier in warmer waters.

Stations with low abundance of *T. longicauda* (Stations 7, 10, 37, 47 and 52) were much alike to the overwintering populations of *T. democratica* described by Heron and Benham (Heron and Benham, 1985), which included scarce solitaries, with only a few of them being mature and with no juvenile stages. Populations with mature solitaries capable of releasing numerous aggregates are considered to be “seed populations”, leading to a rapid increase in salp biomass (Kremer, 2002). This requires a sustained supply of phytoplankton under suitable conditions of salinity, temperature and nutrients.

Differences in population structure and abundance among sampling stations may be due to the patchy distribution of these organisms or due to differences in the degree of population growth and in hydrographic conditions.

CONCLUSION

This is the first study on the development and population structure of *T. longicauda* from the south-western Atlantic Ocean. The maximum abundance, 2970 ind. 1000 m⁻³, was recorded at oceanic stations.

The development of aggregates and solitaries shows differences from other well-known salp species such as *I. zonaria*, *S. thompsoni* and *T. democratica*. The juvenile-/mature ratio of solitaries and aggregates suggests that the studied population was actively reproducing both sexually and asexually, which is also supported by its higher abundance when compared with previous data for the SWAO.

Historical and recent studies suggest that *T. longicauda* may be considered as an oceanic and temperate species because of its presence at the southern range of subtropical waters and northern range of SAW (i.e. cooler and warmer waters, respectively). Unfortunately, the impact of *T. longicauda* on the ecosystem is difficult to assess because sampling of salps is hindered by their temporal and spatial patchy distribution, especially in oceanic areas, because these areas are not routinely sampled. An increase in sampling frequency beyond the shelf break will provide more detailed information on its abundance, distribution, response to environmental variations, changes in population structure and contribution to the carbon budget, among other topics.

SUPPLEMENTARY DATA

Supplementary data is available at *Journal of Plankton Research* online.

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