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ORIGINAL ARTICLE



Mesoscale distribution and population structure of the chaetognath *Serratosagitta tasmanica* (Thomson, 1947) from Southwestern Atlantic Ocean

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ABSTRACT

Although *Serratosagitta tasmanica* is widely distributed, there is little information on how hydrology affects its distribution, abundance and demography. In this study we analyzed the distribution, carbon content and population structure of *S. tasmanica* in the Southwestern Atlantic Ocean. Samples were collected at 34°–39°S (Northern Argentine Continental Shelf in winters of 1999 and 2000) and at 47°–55°S (Southern Argentine Continental Shelf in spring 2005, summer 2006 and winter 2006). The analysis of more than 8500 individuals showed that its dominance decreased spatially from south to north, whereas biomass (mgC/m²) increased temporally by three orders of magnitude between spring (4.06) and summer (12.7). In the southern area the presence of all maturity stages in all seasons suggests year-round reproduction, with maximum reproductive activity in winter. Body length increased with increasing latitude and decreased with temperature. We detected differences in the morphology of seminal vesicles and ovary length between mature specimens. In the northern area all individuals exhibited short-type ovaries whereas in the southern area individuals had either short or long ovaries, suggesting that some individuals of the latter area had been advected from the Southern Pacific Ocean through the water discharged from the Magellan Strait.

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Introduction

Chaetognaths are important components of marine planktonic communities, only outnumbered by copepods. They are active predators in marine food web, having an important impact on copepod populations due to their high grazing pressure (e.g. Froneman et al. 1998), which in time may affect fish stocks by competing for the same prey (Baier and Purcell 1997).

Chaetognaths produce large and fast-sinking faecal pellets (Giesecke et al. 2010) that contribute substantially to the vertical carbon flux (Dilling and Alldredge 1993). Moreover, they are consumed by planktivorous fish (larvae, juveniles and adults) and other pelagic predators (Baier and Purcell 1997). Like other plankton, the distribution, growth, demography and sexual development of chaetognaths are strongly influenced by hydrographic conditions (Pearre 1991; Johnson and Terazaki 2004).

There are more than 120 known species of chaetognaths, 39 of which were found between 0 and 60°S in the South Atlantic, (Casanova 1999; Boltovskoy et al.

2005) and their broad geographic distribution has been described. (e.g. Alvaríño 1969; Mazzoni 1988; Casanova 1999). Among the latter, *Serratosagitta tasmanica* (Thomson 1947) inhabits subantarctic waters of the Pacific, Indian and Atlantic Oceans. It is absent in the Pacific Ocean of the Northern Hemisphere (Alvaríño 1969; Casanova 1999), while in the Atlantic Ocean it occurs in two geographical areas: from 35° to 65°N (temperate waters) and from 35° to 65°S, between the Antarctic and Subtropical Convergences, (i.e. Alvaríño 1969; Ghirardelli 1997; Casanova 1999; Figure 1A).

Notwithstanding its wide distribution, there is limited information on how different water masses and frontal areas affect the distribution, abundance and demography of *S. tasmanica*. In this regard, most data come from the Southeastern Atlantic Ocean and Mediterranean Sea. To our knowledge, only Furnestin (1957) analyzed the population structure of *S. tasmanica* from Moroccan waters. There are scattered data (Figure 1A) on the presence of some mature stages around the Canary Islands (Hernández

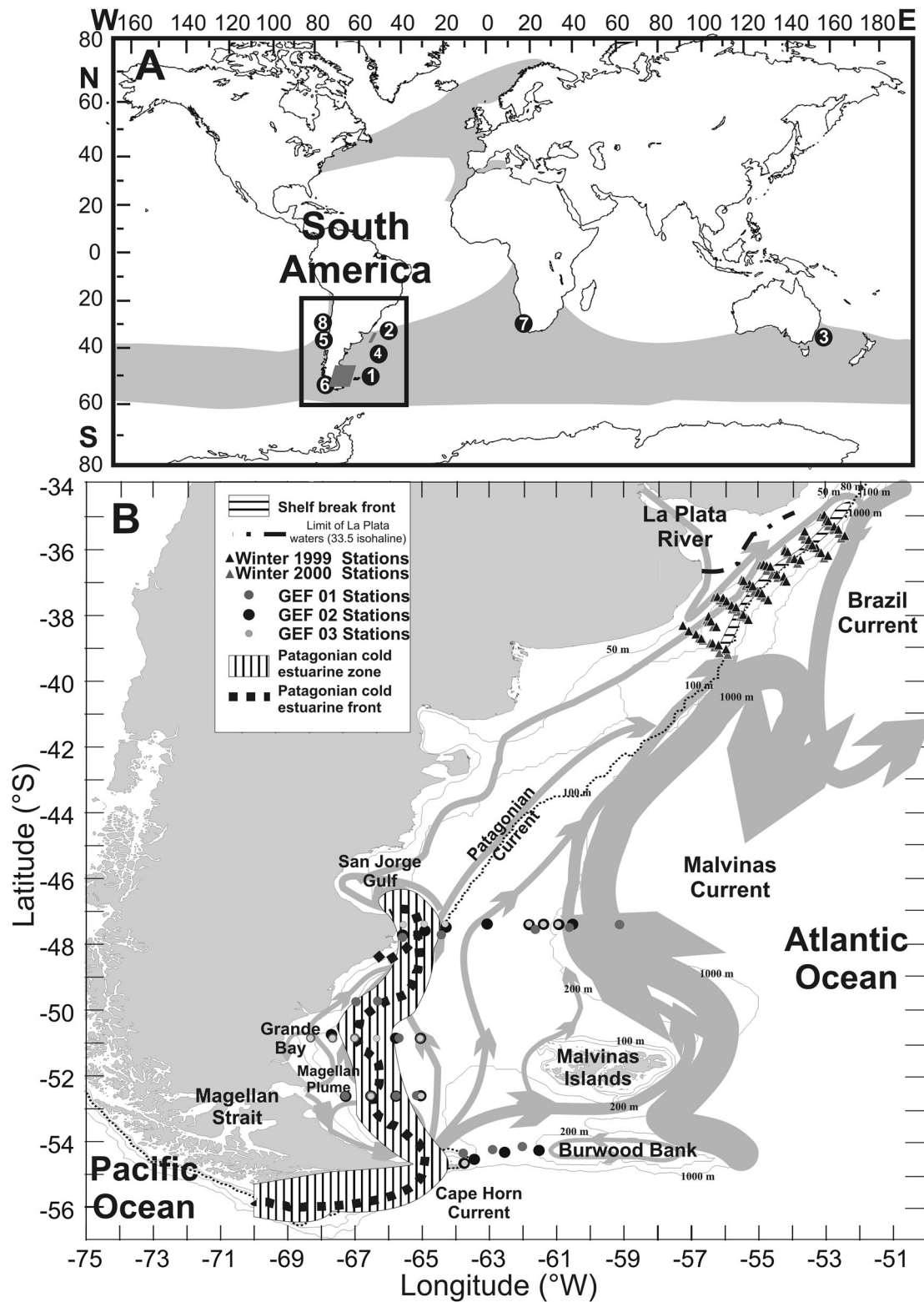


Figure 1. *Serratosagitta tasmanica*. Global geographical distribution and historical data on the distribution of maturity stages (A) Location of sampling stations at the Northern Argentine continental shelf (austral winters of 1999 and 2000) and the Southern Argentine Continental Shelf during cruises GEF 01 (early spring 2005), GEF 02 (late summer 2006) and GEF 03 (late winter 2006). (B) 1. Data Southern Argentine Continental Shelf (present study); 2. Northern Argentine Continental Shelf (present study); 3. Thomson 1947; 4. Boltovskoy 1974; 5. Fagetti 1968; 6. Ghirardelli 1997; 7. Gibbons 1992; 8. Fagetti 1958.

and Lozano 1984), near South African coasts (Gibbons 1992, 1994), in the western Mediterranean Sea (Camiñas 1985) and in the South Pacific Ocean (Thomson 1947; Fagetti 1968; Ahumada 1976).

The aim of the present work was to study the demography and mesoscale distribution of *S. tasmanica* in the Southwestern Atlantic Ocean, analysing its distribution, population structure and carbon content.

Materials and methods

Study area

The Southwestern Atlantic Ocean (SWAO) is characterized by an extensive continental shelf (~1,000,000 km²) with different water masses originated by dilution of open ocean waters of the western boundary currents in the South Atlantic Ocean (Piola and Rivas 1997), and by the presence of several frontal systems located at the continental shelf and shelf-break (Acha et al. 2004).

The upper ocean circulation is dominated by the presence of the warm and salty southward flowing of the Brazil Current (BC) and the cold and relatively fresh northward flow of the Malvinas Current (MC; Figure 1B). The BC, the western boundary current associated with the subtropical gyre in the South Atlantic, turns southeast at ~38°S. The MC originates from a branch of the Antarctic Circumpolar Current, the Cape Horn (Cabo de Hornos) Current which meets the Burdwood Bank (Banco Namuncurá) after crossing the Drake Passage, and bifurcates into two branches: the eastern and western branches (Figure 1B). The eastern branch moves along the edge of the continental slope while the western branch moves northwards over the continental shelf, mixing all along the way with relatively fresher waters from the Magellan Strait, ice melting and freshwater discharges from rivers such as Rio de la Plata (RdP, Piola and Gordon 1989; Piola and Rivas 1997; Guerrero et al. 1999). South of ~49°S the interaction of tidal currents and the Magellan Strait discharge generates the Patagonian Current (Palma et al. 2008; Figure 1B), which moves NNE carrying subantarctic water. North of 38°S the major hydrographic feature is the Rio de la Plata estuary (Figure 1B), which discharges over the continental shelf. The contact between these different water masses along with the prevalent westerly winds and high tidal amplitudes promote the formation of different fronts over the continental shelf and the continental shelf-break (Acha et al. 2004; Sabatini et al. 2004, 2012). These fronts are known to influence the distribution and abundance of phyto-

and zooplankton (e.g. Mianzan and Guerrero 2000; Sabatini and Alvarez-Colombo 2001; Acha et al. 2004). The shelf-break front separates the subantarctic shelf waters (SASW) from the subantarctic waters of the Malvinas Current (SAW; Palma and Matano 2012). The geographical location of the shelf-break front may vary according to the dynamics of the Malvinas Current, for which cyclical variations have been reported (Olson et al. 1988). This front is located between the 80 and 100 m isobaths during winter (Acha et al. 2004). At the southern Patagonian shelf, the 100 m isobath corresponds approximately to the location of the Atlantic Patagonia cold estuarine front (Acha et al. 2004) or Magellan Salinity Front (Sabatini et al. 2012) a typical mid-shelf water mass boundary front (Sabatini et al. 2004).

The BC and MC meet offshore at ~35°S forming the Brazil-Malvinas Confluence, one of the most dynamically active regions in the World Ocean.

Field sampling

Chaetognaths were sampled from southern (SACS, from 47° to 55°S and 69° to 59°W) and northern (NACS, from 34°S to 39°30'S and 52° to 57°W) sections of the Argentine Continental Shelf in the SWAO. At SACS, 51 samples were collected aboard the Research Vessel 'ARA Puerto Deseado' along 4 transects (Figure 1B) during early austral spring 2005 (GEF 01, October 16 to 26), late summer 2006 (GEF 02, March 13 to 26) and late winter 2006 (GEF 03, September 10 to 20). At NACS, 117 samples were taken aboard the 'RV Holmberg' along 8 major transects (T1 to T8) during the austral winters of 1999 (June 5–13) and 2000 (July 20–31) (Figure 1B). Zooplankton sampling was conducted using a Nackthai sampler towed obliquely from near bottom to surface and from shallow waters towards the 200 m isobath at ca. 1.5–2 kts. A net of 20 cm mouth diameter was fitted with a 400-µm mesh net. On all occasions, filtered volumes were estimated by a digital flowmeter mounted in the sampler and temperature and salinity were recorded with a Sea-Bird 911 CTD from near bottom to surface (see vertical profiles Daponte et al. 2011, Sabatini et al. 2012, 2016). Samples were preserved in 5% buffered formaldehyde.

Sample analysis

Chaetognaths were sorted out and identified to species level according to Bieri (1991), more than 8500 specimens of *Serratosagitta tasmanica* were considered for

this study. Density per sample (ind/m^3) was standardized to number of individuals per m^2 (ind/m^2).

The following parameters were measured for each individual: body length (L: from the top of the head to the end of the tail excluding the caudal fin; ± 0.1 mm accuracy), ovary length (OL) and oocyte diameter (OD). In addition, the morphology of the seminal vesicles was examined and the Ovary Index (OI, Furnes-[tin 1957](#)) was estimated as $\text{OI} = \text{OL} \cdot 100 / \text{L}$.

Dry weight (expressed as mg) was obtained from body length (L, in mm) using the following relationship: $\log(\text{DW}) = 3.8747 \cdot \log(\text{L}) - 2.0471$ ([Daponte et al. 2011](#)); carbon content was calculated as $(33.5 \pm 5.4) \% \text{DW}$ ([Conway and Robins 1991](#)). Carbon biomass per sample was also standardized to mgC/m^2 . Damaged specimens that could not be identified to species level or measured were excluded from the analysis of carbon biomass.

Specimens were classified into four (I-IV) maturity stages (modified from [Alvariño 1993](#)) under low magnification (6–50 X) without special staining methods. These were characterized as follows: (I) ovaries not visible or rudimentary, tail segment empty, without seminal vesicles; (II) ovaries thin and short, eggs small, tail segment opaque, seminal vesicles beginning to develop; (III) ovaries thin but variable in length, oocytes of variable diameter, seminal vesicles more developed, with variable amount of sperm; and (IV) ovaries thick and long; eggs enlarged, seminal vesicles well developed, filled with sperm or empty.

Density and biomass values of *S. tasmanica* were plotted and its seasonal distribution was described using non-parametric statistics.

Two-factor fixed effects ANOVA models were used to test for significant differences in log-transformed values of density and biomass between the NACS and SACS areas, in order to analyse potential changes in the spatial and temporal distribution of *S. tasmanica*. The factors were season/year (GEF and Holmberg cruises) and either transect or water mass type (Coastal Water, CW and Middle-Outer Shelf Waters, MOSW), separated by the frontal zones described above.

The distributions of body length and maturity stage were plotted and compared between GEF cruises by the Kolmogorov–Smirnov two-sample test ([Sokal and Rohlf 1995](#)). The spatial and temporal distributions of body length were analyzed with a two-factor (season and water mass type) fixed-effect ANOVA on ranks. Similar analyses were performed on body length but considering the four maturity stages of *S. tasmanica*. In these cases, factors used to analyse temporal distribution were maturity stage and season and the factor

used for spatial distribution in each season was water mass type. The ovaric index was compared among seasons using a two-factor (maturity stage and season) fixed-effect ANOVA on ranks. When significant differences were detected using ANOVA, *a posteriori* comparisons were carried out using Tukey's HSD test for unequal samples ([Zar 1999](#)).

Results

Hydrography

Southern Argentine Continental shelf (SACS)

Temperature distribution varied from NW to SE according to the season with highest values in summer and lowest in early spring. Salinity increased from CW towards the continental slope but its values were conservative along the three sampling periods ([Table I](#)). This is an agreement with the vertical profiles in [Sabatini et al. 2016](#), who classified the water masses according to salinity as the MSW (Magellan Strait Water, $S < 33.4$) located near shore, the SASW (Subantarctic Shelf Water, $33.4 < S < 34.0$) in middle-shelf waters and the SAW (Subantarctic Water, $S > 34.0$) at deep stations far offshore.

Analysis of the data from the CTD sensor indicated a weak stratification in early spring (GEF 01), which increased by the end of summer (GEF 02). In this season, a strong thermocline was present in the northern section, which became weaker southwards. The conditions at the end of winter (GEF 03) were similar to those found in late spring, except for a cold water intrusion coming from the Magellan Strait, flowing northwards along the coast and extending for several kilometres on the continental shelf (additional information in [Charo and Piola 2013](#); [Sabatini et al. 2016](#)).

Northern Argentine Continental shelf (NACS)

Surface temperature and salinity differed depending on the main water masses and years analyzed. In 1999 ([Table I](#)) temperature ranged between 13°C (in coastal waters and at the offshore station of T1) and 8°C (in offshore waters along T6 and T8). In middle shelf waters, surface salinities between 32.4 and 33.2 indicated the presence of SASW, whereas temperatures between 6 and 9°C and salinities between 33.8 and 34.0 indicated the presence of MC (SAW) at offshore stations of the southern transects (T5, T6 and T8). The most offshore station of T1 was the only one showing temperatures higher than 15°C and salinities higher than 34.3, suggesting the presence of Sub-Tropical Shelf Waters (STSW) of the Brazil Current ([Möller et al. 2008](#)). In 2000 ([Table I](#)) water temperature was lower

Table I. Temperature and salinity range from coastal waters (CW) toward the shelf break for Southern Argentine Continental Shelf (SACS) and Northern Argentine Continental Shelf (NACS).

| | SACS | | | NACS | |
|------------------------|-----------------------|----------------------|----------------------|-------------|-------------|
| | Early Spring (GEF 01) | Late Summer (GEF 02) | Late Winter (GEF 03) | Winter 1999 | Winter 2000 |
| Temperature range (°C) | 4.5–7.2 | 5.5–14.5 | 5.2–7.0 | 6–15.5 | 7.5–10.5 |
| Salinity range | 32.6–34.2 | 32.7–34.1 | 32.7–34.1 | 32.4–34.3 | 33.8–34.7 |

than in 1999 over most of the shelf, decreasing from the coast to the continental slope (10.5°C – 7.5 °C). Salinity was relatively homogeneous over most of the shelf (33.8–33.9) indicating the presence of SASW, whereas values were up to 34.7 in offshore waters, corresponding to SAW (see vertical profiles in Daponte et al. 2011). During winter 2000 the shelf front was not detected.

Distribution of Abundance and Biomass

At SACS *Serratosagitta tasmanica* represented between 86 and 95% of total chaetognaths recorded from spring to late winter. There were significant differences in density and biomass among seasons (Tables II and III, Figure 2A–F), with peaks of up to 404 ind/m² and 12.7 mgC/m², respectively, at the end of summer (Tukey's HSD, $P < 0.035$), values dropped to a minimum in early spring and were intermediate in late winter (Table III). Both variables were significantly higher in MOSW than in CW (Table IV).

At NACS, the studied species represented between 10% and >60% of total chaetognaths found in the winters of 1999 and 2000, respectively. In both years it was found in 79% of total samples. Density and biomass values were substantially higher in 2000 (>1100 ind/m² at T1 and >83 mgC/m² at T5) than in 1999 (up to 204 ind/m², > 8 mgC/m² at T5; Tables II and III; Figure 2G,H). Both variables were significantly higher in MOSW than in CW (Table IV).

Body length distribution of *Serratosagitta tasmanica*

Body length varied both seasonally and between years. At SACS it ranged between 4.8 and 19 mm in early spring, 4.8–21.20 mm in late summer and 2.4–15.04 mm during the following winter (Table V). The Kolmogorov–Smirnov two-sample test showed highly significant differences ($P < 0.001$) among all frequency distribution patterns. The highest body length frequencies showed the following seasonal variations: 12–13 mm in early spring, 14–16.9 mm in late summer and 5–9 mm in winter (Figure 3A–C). Mean body length of the *S. tasmanica* population increased from early spring to late summer and dropped markedly

during winter. The individuals from both CW and MOSW showed seasonal variations in body length (Table V), with significant differences between CW and MOSW within and among seasons (two-way ANOVA on ranks, $F_{2,3910}:116$, $P < 0.0001$). Larger specimens were recorded in early spring and late summer in CW and during winter in MOSW (Figure 4), with a dramatic decrease in total body length as previously observed in late winter (Figure 3A–C).

At NACS, the length-frequency distributions were significantly different between years (Kolmogorov–Smirnov two-sample test, $D_{\max} = 0.149$, $P < 0.001$). Values ranged between 3.2 and 18.08 mm in 1999 (highest frequencies varied between 10 and 11 mm) and between 3.2 and 18.4 mm in 2000 (highest frequencies were 8–9 mm and 12–13 mm; Figure 3D,E).

Maturity stages of *Serratosagitta tasmanica*

All maturity stages (I to IV) were found in both NACS and SACS areas (Figure 5). At SACS, stage frequencies differed among seasons: stage II (> 41%) was more frequent in early spring, stages III (> 26%) and IV (>44%) peaked in late summer and stage I largely dominated (>80%) in late winter (Figure 5). At NACS, immature stages represented a small portion of the population, whereas stages III and IV accounted for 77% and 71% of the population in 1999 and 2000, respectively.

There was a significant increase in body length from stage I to IV for all cruises from NACS and SACS (Figures 3–6; Table VI), except for late winter 2006 at SACS, when it showed a slight increase (Figure 6A). Body length values did not follow a normal distribution for any of the maturity stages and differed significantly among seasons (two-way ANOVA on ranks, $F_{6,3903}:7.81$, $P < 0.0001$) and years (two-way ANOVA on ranks, $F_{3,4607}: 29.35$, $P < 0.0001$). Values were similar for spring and summer, which in turn were significantly higher than those obtained in winter (Table VI), (Figure 6A; Tukey's HSD, $P < 0.001$). Maturity stages showed significant differences in body length between CW and MOSW (Table VI, Figure 6B–D) at SACS. Stages III and IV (in early spring) and stages II and III (in late summer) were significantly longer in

Table II. Summary of descriptive statistics for density and biomass values of *Serratosagitta tasmanica* according to sampling area and season.

| | SACS | | | NACS | |
|--------------------------------|-----------------------|----------------------|----------------------|-------------|-------------|
| | Early Spring (GEF 01) | Late Summer (GEF 02) | Late Winter (GEF 03) | Winter 1999 | Winter 2000 |
| <i>n</i> | 19 | 19 | 14 | 48 | 40 |
| Frequency (%) | 100 | 100 | 93 | 79 | 95 |
| Density (ind./m ²) | | | | | |
| Median | 1.37 | 29.48 | 11.28 | 24.67 | 51.57 |
| Range(Min-Max) | 0.11–87.9 | 0.37–404.1 | 0–248.9 | 0–203.5 | 0–1174 |
| 25% Quartile | 0.50 | 2.06 | 2.48 | 6.87 | 18.34 |
| 75% Quartile | 16.79 | 147.4 | 21.77 | 54.30 | 193.66 |
| Biomass (mgC/m ²) | | | | | |
| Median | 0.07 | 1.98 | 0.06 | 0.38 | 2.09 |
| Range(Min-Max) | 0.004–4.06 | 0.009–12.7 | 0–2.09 | 0–8.02 | 0–83.4 |
| 25% Quartile | 0.01 | 0.11 | 0.02 | 0.08 | 0.58 |
| 75% Quartile | 0.64 | 4.44 | 0.35 | 1.46 | 7.19 |

Note: SACS: Southern Argentine Continental Shelf, and NACS: Northern Argentine Continental Shelf.

CW than in MOSW (Figure 6B,C). During winter, stage I specimens were significantly longer in MOSW than in CW, whereas no differences between these areas were found for the other stages (Figure 6D). Note-worthy, no stage IV specimens were recorded in CW samples. During late winter 2006 at SACS, some (~ 5.5%) small specimens (body length < 4 mm) lacking the caudal septum were collected; they were assigned to 'larval stage' (Figure 3C). At NACS, mature specimens showed higher body length values in 2000 (cooler waters) than in 1999 (warmer waters; Table VI).

The ovaric index increased significantly from stages I to IV in early spring and late summer and from stages I to III during winter (Figure 7). All stages showed a significantly higher index in late summer than in the other seasons (Figure 7).

Sexually mature specimens (stage IV) showed variability in OL, diameter of mature oocytes and morphology of seminal vesicles. Oocyte diameter generally ranged between 0.1 and 0.2 mm, reaching up to 0.35 mm in a few specimens. Some specimens possessed long ovaries extending up to the posterior

end of the ventral nervous ganglion (long ovary type) while others had short ovaries just reaching the posterior end of the anterior fin (short ovary type) (Figure 8). Both ovary types contained mature oocytes of similar size. Specimens with both ovary types were mainly found in the southern area in spring and summer, with seasonal frequency variations. Large ovaries were present in 18% and 45% of stage IV specimens in early spring and late summer, respectively. Seminal vesicles also showed morphological differences, with the main axis being parallel to the body axis in 90% of the specimens and perpendicular to it or in an intermediate position in the rest of the sample (Figure 8).

Discussion

Distribution of *Serratosagitta tasmanica*

Serratosagitta tasmanica inhabits subantarctic waters around the Antarctic Ocean extending to southern areas of the Indian, Pacific and Atlantic Oceans (Alvarinho 1969). It is abundant in the Southeastern Pacific Ocean (Palma and Silva 2004) and the Magellan Strait (connecting the Pacific and Antarctic Oceans) with ~ 1000 ind/m³ and a frequency of occurrence ~75% (Ghirardelli 1997). With regard to the circulation of water masses (Introduction), Mazzoni (1990) suggested that the Magellan Strait and Beagle Channel would be the entry routes of this species from the southeastern Pacific into the Southwestern Atlantic Ocean (SWAO). Our results showed that *S. tasmanica* is a frequent and abundant species from 34° 30' S to 55°S in the shelf sector of the SWAO. Its dominance increased from north to south, representing between 10% and 70% of total chaetognaths at NACS and more than 90% at SACS. Its abundance along inshore-offshore transects and from north to

Table III. Analysis of density and biomass of *Serratosagitta tasmanica*.

| | SACS | | | NACS | | |
|-------------------|------|-------|--------|------|-------|---------|
| | d.f. | ratio | P | d.f. | ratio | P |
| Factor – DENSITY | | | | | | |
| DATA | | | | | | |
| Cruise | 2.38 | 6.033 | 0.005* | 1.67 | 6.44 | 0.013* |
| Transect | 3.38 | 2.51 | 0.073 | 7.67 | 4.20 | 0.001* |
| Cruise x Transect | 6.38 | 1.64 | 0.162 | 7.67 | 1.79 | 0.103 |
| Factor – BIOMASS | | | | | | |
| DATA | | | | | | |
| Cruise | 2.38 | 6.01 | 0.005* | 1.67 | 13.75 | <0.001* |
| Transect | 3.38 | 1.94 | 0.139 | 7.67 | 1.52 | 0.171 |
| Cruise x Transect | 6.38 | 1.82 | 0.120 | 7.67 | 0.66 | 0.699 |

Note: Summary of two-way ANOVA with fixed factors (Cruise and Transect) at SACS: Southern Argentine Continental Shelf and NACS: Northern Argentine Continental Shelf. Density data were log-transformed. d. f.: degrees of freedom; *Significant P values.

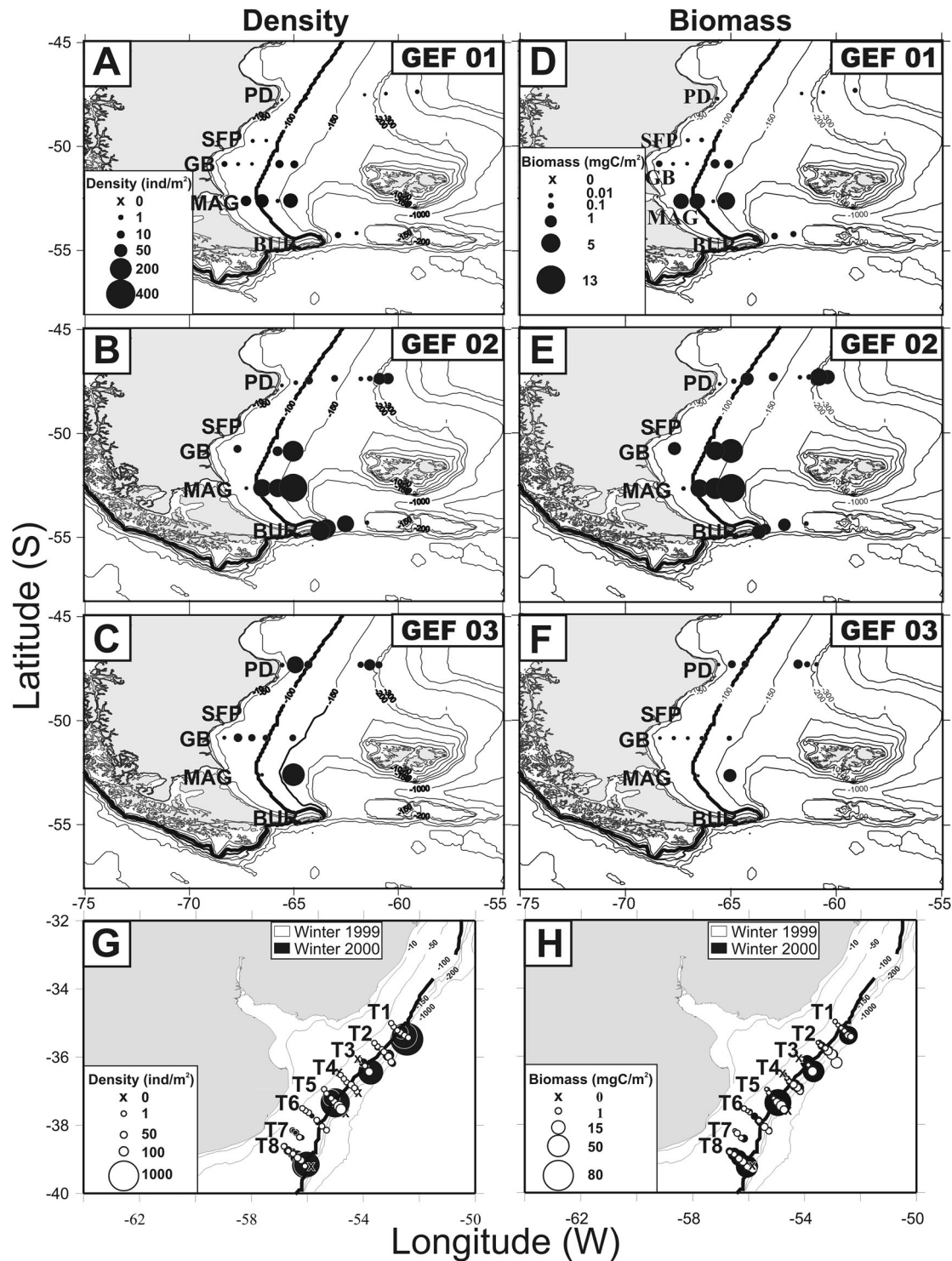


Figure 2. Density and biomass of *Serratiasagitta tasmanica* at the southern and northern Argentine Continental Shelf. Density (in ind/m³) in early spring (GEF 01), late summer (GEF 02) and late winter (GEF 03) (A-C), biomass (in mgC/m³) in early spring (GEF 01), late summer (GEF 02) and late winter (GEF 03) (D-F), density (ind/m³) in winter 1999 and 2000 (G) and biomass (mgC/m³) in winter 1999 and 2000 (H). BUR: Burwood Bank transect, GB, Grande Bay transect, MAG: Magellan Strait transect, PD: Puerto Deseado transect. T1-T8: Transects 1 to 8.

south appeared to be influenced by physical process. In NACS the Río de la Plata is characterized as a biogeographic boundary between communities of

brackish and oceanic waters (Carreto et al. 2003). Its effect on the medium and outer shelf waters (RDP plume) varied seasonally having smaller influence in

Table IV. Analysis of density and biomass of *Serratosagitta tasmanica*.

| | SACS | | | NACS | | |
|----------------------------|------|-------|--------|------|-------|---------|
| | Df | ratio | P | Df | ratio | P |
| Factor – DENSITY DATA | | | | | | |
| Cruise | 2.46 | 2.78 | 0.072 | 1.79 | 4.84 | 0.031* |
| Water mass type (CW, MOSW) | 1.46 | 6.17 | 0.016* | 1.79 | 8.51 | 0.046* |
| Cruise x Water mass type | 2.46 | 0.49 | 0.612 | 1.79 | 0.39 | 0.530 |
| Factor BIOMASS DATA | | | | | | |
| Cruise | 2.46 | 3.75 | 0.059 | 1.78 | 11.24 | <0.001* |
| Water mass type (CW, MOSW) | 1.46 | 3.32 | 0.044* | 1.78 | 5.22 | 0.025* |
| Cruise x Water mass type | 2.46 | 0.34 | 0.708 | 1.78 | 1.46 | 0.230 |

Note: Summary of two-way ANOVA with fixed factors (Cruise and water mass type) at SACS: Southern Argentine Continental Shelf and NACS: Northern Argentine Continental Shelf. CW: Coastal Water, MOSW: Middle-Outer Shelf Water. d.f.: degrees of freedom, *Significant P values.

winter. In particular during winter 1999, RdP's plume was more limited than in previous winters (Piola et al. 2008). Although termohaline values allow the identification of RdP's plume waters (Möller et al. 2008) these values were not found in the sampling area during winters of 1999 and 2000. *Serratosagitta tasmanica* abundances increased from the middle shelf to the shelf break stations. This, together with an increase in salinity values from 32.7 (at 50 m isobath) to 34.0 (Daponte et al. 2011) suggested that the stations were located further east of the influence area of the RdP's plume.

At SACS, lower abundances of *S. tasmanica* on the west side (CW) of the Magellan Salinity Front could be related to the lower salinity values recorded (< 32.7) which may result from the influence of freshwater discharges of many Patagonian rivers (e.g. Coig, Gallegos, Deseado and Santa Cruz rivers). In contrast, higher abundances of *S. tasmanica* were recorded on the east side (MOSW) of the Magellan Salinity Front at salinities between 33.4 and 34.0 typical of SASW. In this area, abundances were particularly higher along southern transects, which are characterized by intense vertical

mixing (Sabatini et al. 2016), than along transects with vertically stratified waters. Similar results were found by Liang and Vega-Pérez 1994 who reported in Brazilian waters higher abundances of chaetognaths in areas with intense vertical mixing than in stratified waters. Intense vertical mixing provide nutrient-rich water for the growth of primary producers which in turn supports greater abundance of mesozooplankton, while vertical stratification of the water column produces a nutrient deficiency at the uppermost layers that leads to a limitation of primary production that may support only low production of mesozooplankton (Kiorbe and Nielsen 1990). Similar differences in species assemblages, abundance and biomass (as mgC/m²) of other mesozooplanktonic groups were found between CW and MOSW at SACS (Sabatini et al. 2016) and between coastal and shelf waters at NACS (e.g. Mianzan and Guerrero 2000; Viñas et al. 2002)

Population structure and maturity stages

The presence of all maturity stages and a constant presence of adults from spring to winter suggest that *S. tasmanica* reproduces all year round, with highest abundance of juveniles being observed in late winter. These results are in agreement with those reported by Furnestin (1957) in Moroccan Atlantic waters, which is to our knowledge the first study dealing with the population structure of this species. When considering all seasons analyzed at SACS, the presence of newly hatched individuals (< 4 mm) along with the highest frequency of juveniles (> 79%) in late winter suggests that it is the period of higher reproductive activity. Moreover, the abundance of juveniles and the decline in mature individuals by the end of the winter suggest a population turnover. In addition, the scarcity of stage IV individuals (with larger sizes, ripe ovaries and filled or empty seminal vesicles) in this

Table V. Summary of non-parametric descriptive statistics of body length distribution of *Serratosagitta tasmanica* according to sampling area, season and water mass type.

| | SACS | | | | | | NACS | | |
|-------------------|-----------------------|-------|----------------------|-------|----------------------|-------|-------|-------|-------|
| | Early Spring (GEF 01) | | Late Summer (GEF 02) | | Late Winter (GEF 03) | | 1999 | | 2000 |
| | CW | MOSW | CW | MOSW | CW | MOSW | SASW | SAW | SASW |
| n | 169 | 733 | 216 | 1851 | 379 | 568 | 273 | 258 | 1929 |
| Total length (mm) | | | | | | | | | |
| Median length | 15.00 | 12.00 | 15.36 | 14.08 | 6.40 | 8.32 | 10.40 | 11.20 | 11.52 |
| Modal length | 16.00 | 12.00 | 15.20 | 14.88 | 4.00 | 11.36 | 10.40 | 12.00 | 13.60 |
| Minimum length | 7.00 | 4.80 | 5.92 | 4.80 | 2.56 | 2.40 | 4.00 | 3.2 | 3.2 |
| Maximum length | 19.00 | 17.20 | 21.10 | 21.20 | 15.04 | 13.76 | 16.80 | 18.08 | 18.40 |
| 25% Quartile | 11.20 | 10.00 | 14.48 | 12.00 | 4.80 | 6.08 | 8.32 | 9.60 | 8.48 |
| 75% Quartile | 16.00 | 13.10 | 16.56 | 15.68 | 8.48 | 10.56 | 12.00 | 12.48 | 13.60 |

Note: SACS: Southern Argentine Continental Shelf, NACS: Northern Argentine Continental Shelf, CW: coastal water, MOSW: Middle-Outer Shelf Water, SAW: Subantarctic Water, SASW: Subantarctic Shelf Water.

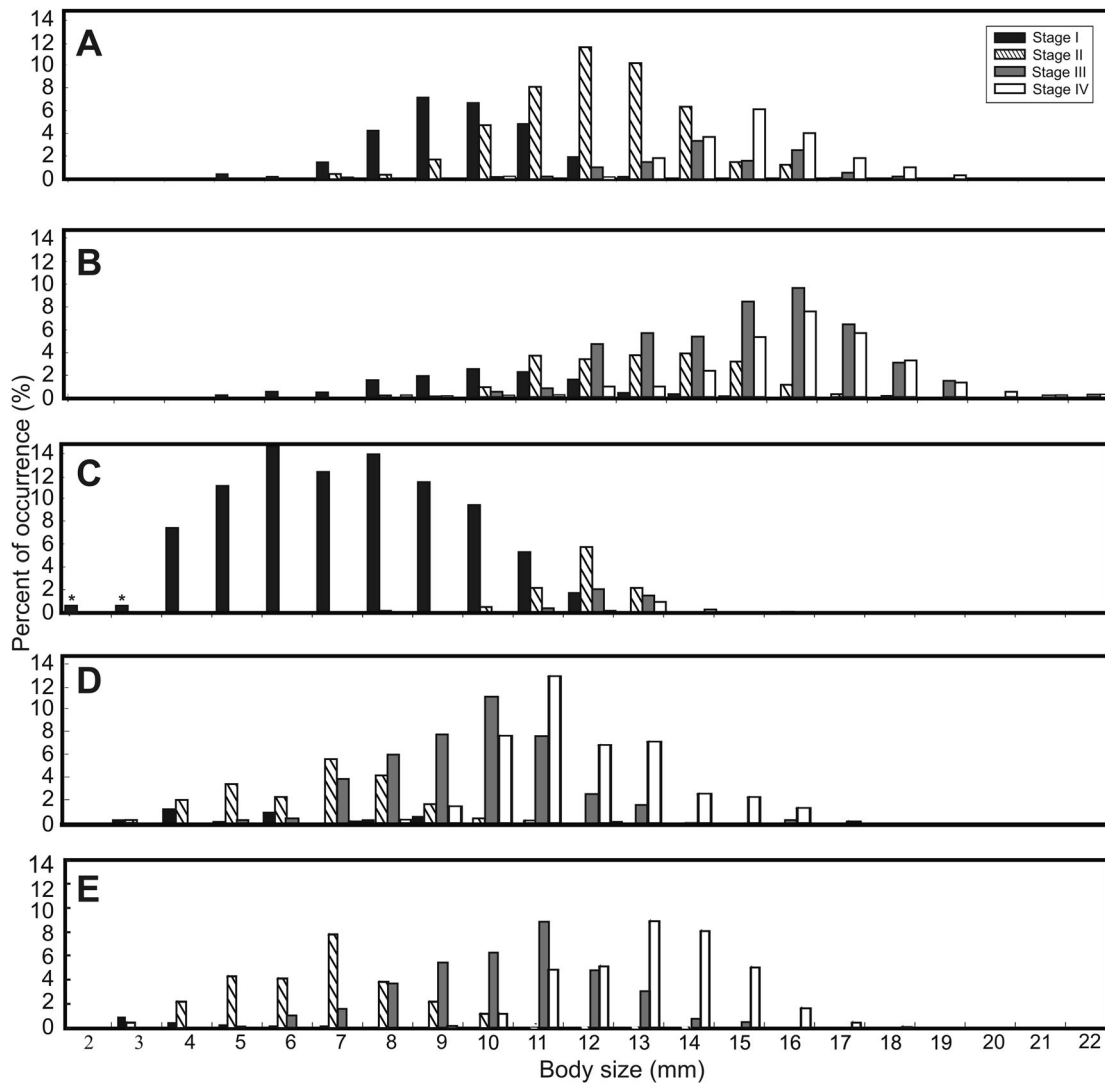


Figure 3. Size distribution of *Serratosagitta tasmanica* at the Southern (A-C) and Northern (D, E) Argentine Continental Shelf. Early spring (GEF 01) (A), late summer (GEF 02) (B), late winter (GEF 03) (C), winter 1999 (D), winter 2000 (E). *larval stage.

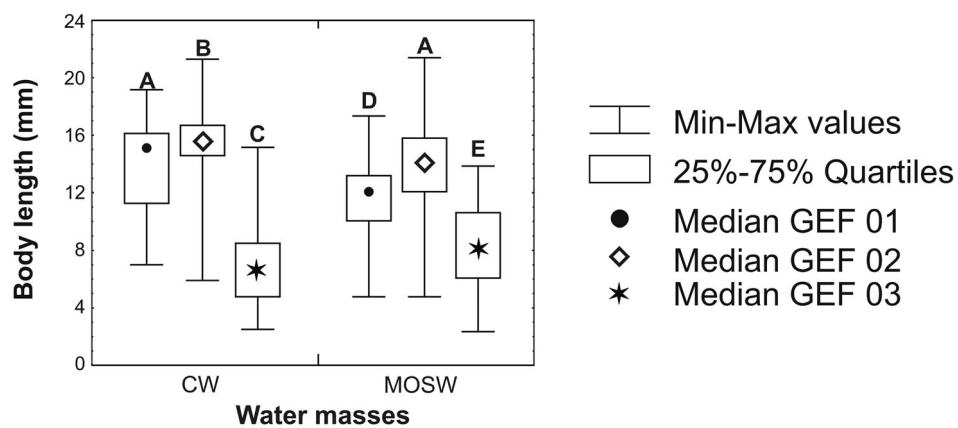


Figure 4. Non-parametric distribution of body length in Coastal (CW) and Middle-Outer shelf (MOSW) water masses. Different letters indicate a significant difference ($P \leq 0.05$).

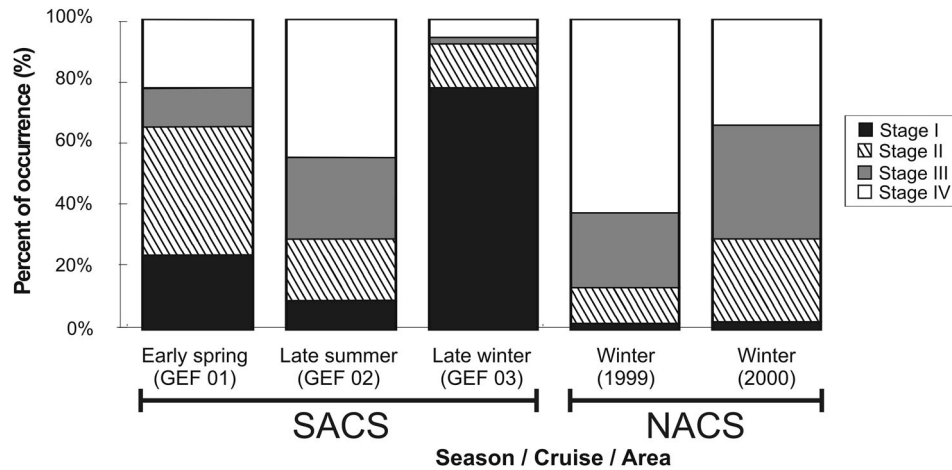


Figure 5. Percentage of occurrence of maturity stages of *Serratosagitta tasmanica* at the Southern Argentine Continental Shelf in early spring (GEF 01), late summer (GEF 02) and late winter (GEF 03).

season could be related to their death after breeding, as observed for other chaetognath species (e.g. Øresland 1986). In turn, the larger individuals sampled at the end of spring and summer could have come from larvae that had hatched during autumn and experienced longer development in the colder waters of winter.

Continuous reproduction and further development may account for the wide range of sizes observed for each stage, which could lead to size overlap in all seasons.

At NACS, the number of larvae and juveniles was probably underestimated due to the use of coarse mesh sizes. However, the analysis of size distribution

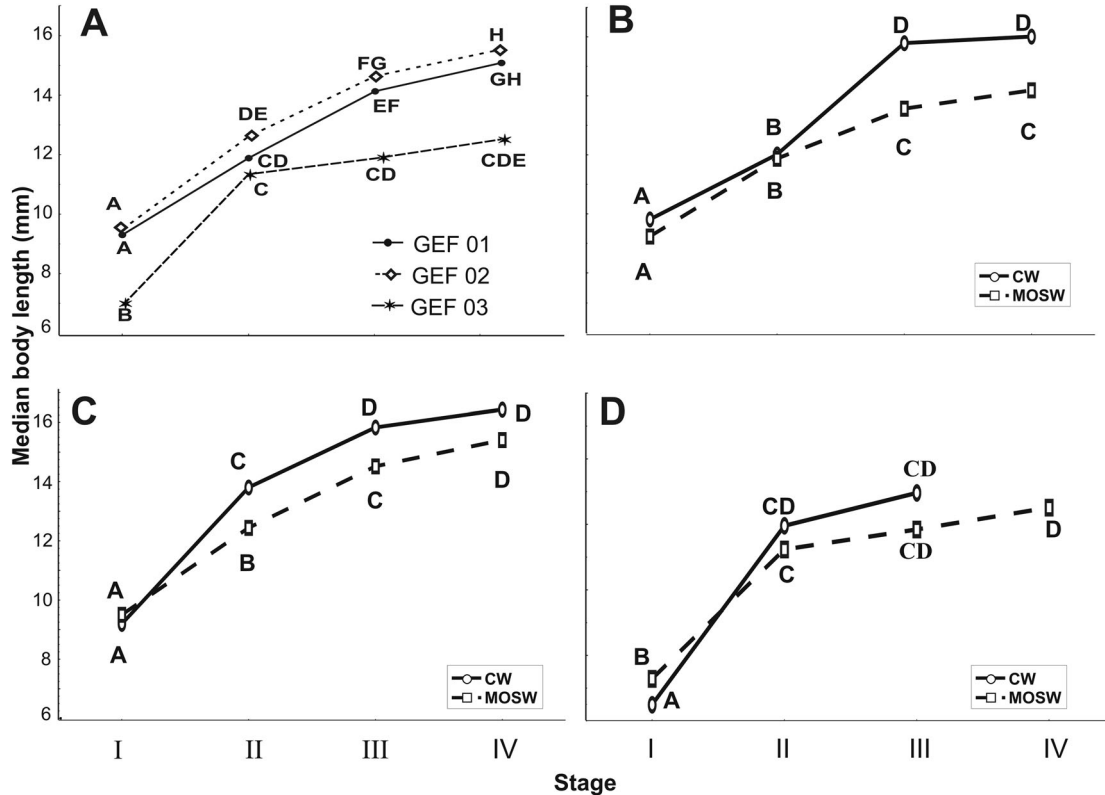


Figure 6. Distribution of median body length for each maturity stage of *Serratosagitta tasmanica* among GEF cruises (A), and between Coastal (CW) and Middle-Outer shelf (MOSW) water masses for early spring (GEF 01) (B), late summer (GEF 02) (C), late winter (GEF 03) (D). Different letters indicate a significant difference ($P \leq 0.05$).

Table VI. Summary of non-parametric descriptive statistics of body length distribution of *Serratosagitta tasmanica* for each maturity stage according to sampling area and season.

| Stage | SACS | | | | | | | | | | | | NACS | | | | | | | | | | | |
|-------------------|-----------------------|-------|-------|-------|----------------------|-------|-------|-------|---------------------|-------|-------|-------|-------------|-------|-------|-------|-------------|-------|------|-------|-------|--|--|--|
| | Early Spring (GEF 01) | | | | Late Summer (GEF 02) | | | | Late Winte (GEF 03) | | | | Winter 1999 | | | | Winter 2000 | | | | | | | |
| | I | II | III | IV | I | II | III | IV | I | II | III | IV | I | II | III | IV | I | II | III | IV | | | | |
| n | 237 | 401 | 98 | 166 | 220 | 390 | 908 | 548 | 793 | 101 | 39 | 10 | 24 | 118 | 258 | 263 | 85 | 1043 | 85 | 1423 | 1401 | | | |
| Total length (mm) | | | | | | | | | | | | | | | | | | | | | | | | |
| Median value | 9.05 | 12.00 | 14.00 | 15.00 | 9.60 | 12.64 | 14.88 | 15.68 | 6.72 | 11.36 | 11.84 | 12.48 | 6.24 | 7.36 | 10.32 | 12.00 | 4.16 | 7.36 | 4.16 | 10.88 | 13.60 | | | |
| Minimumvalue | 4.80 | 7.00 | 6.72 | 10.00 | 4.80 | 8.64 | 9.28 | 7.20 | 2.40 | 7.04 | 9.92 | 11.52 | 4.00 | 3.84 | 5.60 | 7.40 | 3.52 | 4.00 | 3.52 | 6.00 | 9.32 | | | |
| Maximumvalue | 12.25 | 16.25 | 18.00 | 19.00 | 14.88 | 17.92 | 21.20 | 21.20 | 12.32 | 15.04 | 13.28 | 13.76 | 13.60 | 11.20 | 16.16 | 17.44 | 8.80 | 14.40 | 8.80 | 16.00 | 18.40 | | | |
| LowerQuartile | 8.20 | 11.00 | 13.00 | 14.00 | 8.16 | 11.20 | 13.12 | 14.56 | 5.12 | 10.88 | 11.36 | 12.16 | 4.36 | 5.76 | 8.96 | 11.20 | 4.00 | 5.80 | 4.00 | 9.60 | 12.64 | | | |
| UpperQuartile | 10.10 | 13.00 | 16.00 | 16.00 | 10.72 | 13.76 | 16.08 | 16.64 | 8.48 | 12.00 | 12.48 | 12.80 | 8.80 | 8.32 | 11.20 | 13.60 | 5.60 | 8.32 | 5.60 | 12.16 | 14.72 | | | |

Note: SACS: Southern Argentine Continental Shelf, NACS: Northern Argentine Continental Shelf, I, II, III, IV: maturity stages.

revealed a high percentage of mature individuals and a small number of larvae and juveniles, suggesting that the onset of hatching is earlier at NACS than at SACS. This would coincide with a differential warming of the sea surface and an earlier onset of phytoplankton bloom in the north (33°S) compared with the south (55°S) of the studied area (Andreo et al. 2016). Coinciding with these results, Sabatini et al. (2012, 2016) reported that at a given time, northern zooplankton populations are generally in a more advanced state of development than those in the south.

Our results suggest that the range of body length is wider for *S. tasmanica* individuals at SACS, with lower SST values (up to 21.2 mm between 5 and 13°C), than at NACS, with higher SST values (up to 17.8 mm between 8 and 15.5°C). In our study, juvenile sizes are comparable to those reported by Ghirardelli (1997) in the Strait of Magellan (5–7 mm) or by Fagetti (1968) in southern Chilean waters (8–10 mm). In addition, the body length of adults is known to increase with decreasing seawater temperature (latitudinal increase), as reported for different locations off the coast of America (Figure 1A, Fagetti 1958, 1968; Ghirardelli 1997) or other continents in the Southern Hemisphere (Gibbons 1994 for Africa; Thomson 1947 for Oceania). A similar pattern is suggested for *S. tasmanica* from warmer waters of the Northern Hemisphere: it reaches up to 17 mm (SST: 14–22.5 °C; Furnestin 1957) in the Moroccan Atlantic Ocean, and up to 8.42 mm around the Canary Islands (SST: 19.5–21.5°C; Hernandez et al. 1997). In addition, our study suggests a tendency of *S. tasmanica* to mature at smaller body sizes at higher temperatures (Figure 9), which is in agreement with results reported for other chaetognath species (Pearre 1991 and references therein). Several studies of chaetognaths showed that different environmental parameters (e.g. temperature, salinity, food availability) play an important role not only in individual morphological features (e.g. Furnestin 1957; Alvarino 1967; Tokioka 1974) but also in population growth and development (e.g. Alvarino 1983; Giesecke and Gonzalez 2008).

Even though chaetognaths prefer to prey upon copepods, their diet varies with age, size and prey. Compared to adults of the same species, larvae and young individuals usually feed on smaller and easy-to-digest prey (Bonnet et al. 2010), such as copepod nauplii, ciliates, dinoflagellates and small meroplankters (e.g. Pearre 1981). Instead, adults prefer copepodites and adult copepods (e.g. Tönnesson and Tiselius 2005). Gibbons (1992) reported that *S. tasmanica* from the Benguela region consumed copepods belonging to the genera *Oithona*, *Metridia*, *Calanus*,

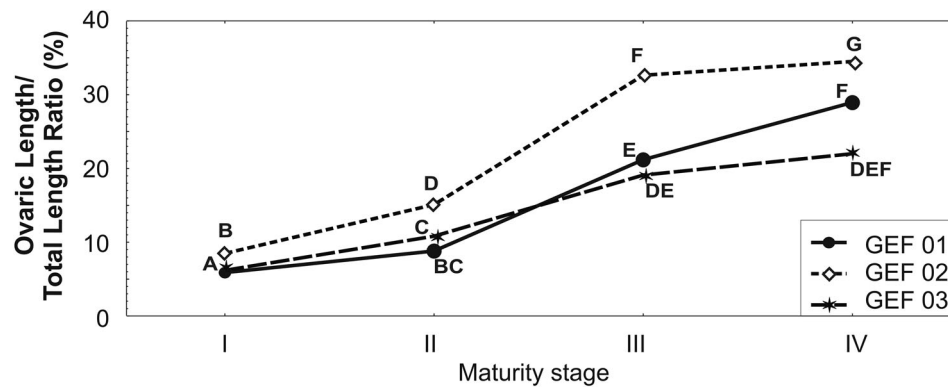


Figure 7. Ovary Index (ovary length:total length ratio) for each maturity stage of *Serratosagitta tasmanica* in early spring (GEF 01), late summer (GEF 02) and late winter (GEF 03). Different letters indicate a significant difference ($P \leq 0.05$).

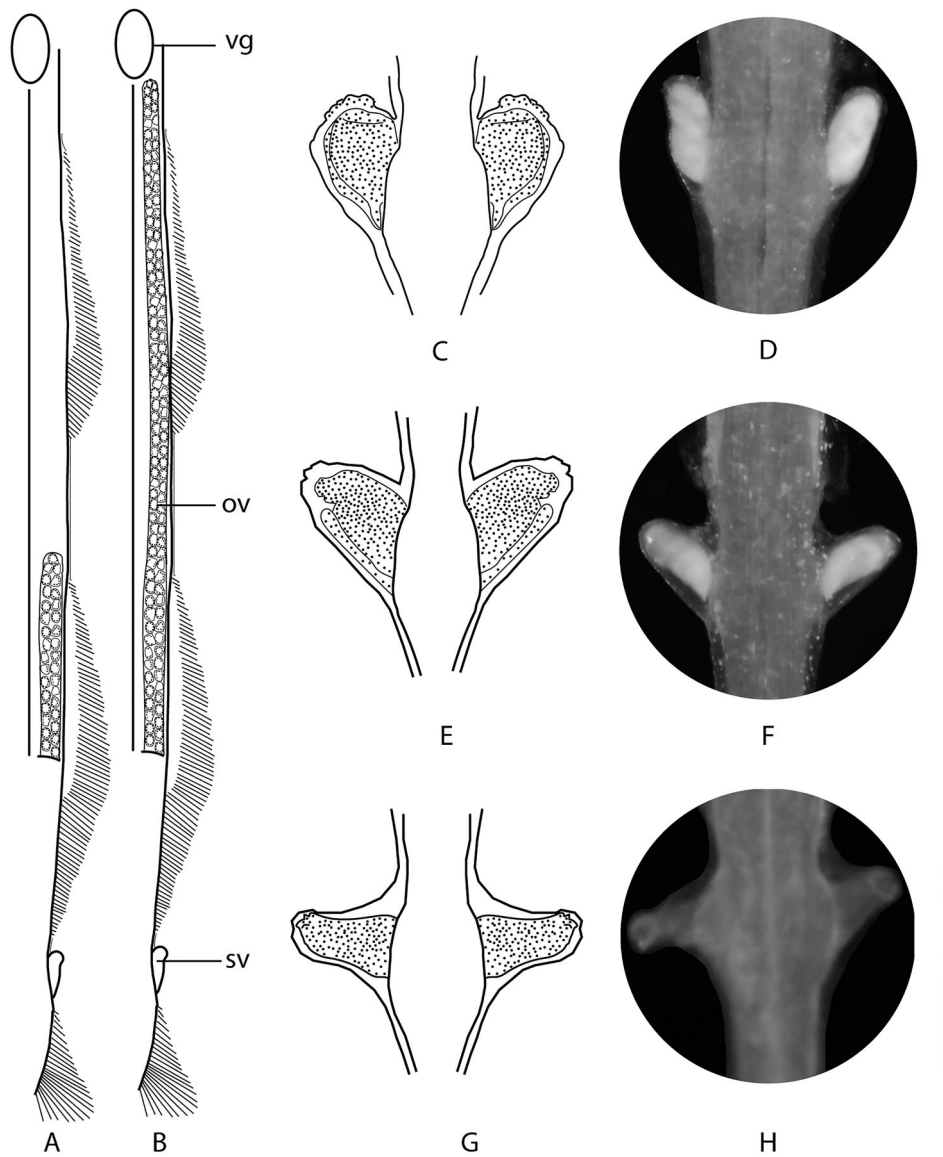


Figure 8. Morphological differences of *Serratosagitta tasmanica*. Sexually mature individuals with short ovaries (A) and long ovaries (B). Seminal vesicles with their longitudinal axis at different angles (C-E).

Paracalanus and *Ctenocalanus*. Members of these taxa were present in copepod assemblages collected on the same cruises as in this study (Sabatini et al. 2016). On this basis, it could be hypothesized that the population density of *S. tasmanica* may increase with increasing density of copepods. However, there was no significant correlation between abundance of chaetognaths and copepods, with higher abundances of chaetognaths being found in areas of moderate copepod abundance. Although chaetognaths are considered opportunistic predators, Casanova et al. (2012) suggested that they may gulp seawater, ingesting dissolved microscopic particulate organic matter produced by viruses and bacteria and this may explain their biological success. In addition, it is possible that chaetognaths also prey on ciliates (Pearre 1981) occurring at high densities during the austral summer in the MOSW area (Santoferrara et al. 2011). The abundance of ciliates, copepodites and copepod nauplii occurring at high densities in the MOSW area (Santoferrara et al. 2011; Sabatini et al. 2012), along with the capacity of chaetognaths to feed on particulate organic matter could provide larvae and juveniles with the energy required to reach maturity and complete their life cycle.

At SACS, *S. tasmanica* biomass increased by three orders of magnitude from spring to summer. This would contribute to the amount of food available for larvae and adults of planktonic fish inhabiting this area and whose spawning seasons are in spring/summer (e.g. *Sprattus fuegensis*, the fuegian sprat) or those whose nursery grounds are between 52°S and 55°30'S (e.g. *Macruronus magellanicus*, the longtail hake).

At NACS, the life-cycle of chaetognaths followed that of copepods. However, the lower abundance in 1999 than in 2000 could be related to a bloom of the salp *lasis zonaria* (Daponte et al. 2011), which covered the entire area. It may have resulted in a dramatic decrease in phytoplankton biomass and subsequent decline in the populations of copepods and chaetognaths.

Morphological differences

It is worthwhile to mention the morphological variations found in stage IV individuals concerning both the appearance of the seminal vesicles (Figure 8C–H) which has been previously reported elsewhere (Boltovskoy 1974; Pierrot-Bults 1976), and the ovary extending up to the ventral ganglion (Figure 8A,B). According to Alvarino (1967), some chaetognath species that attain sexual maturity at different body sizes and ovary lengths may have more than one reproductive cycle. For example, in *S. enflata* fully mature ovaries extend

up to two-thirds of the extent of the posterior fins, to the anterior end of the posterior fins, or to the anterior fins depending on whether the individuals undergo their first, second or last maturity cycle, respectively (Alvarino 1983 and references therein). The presence of few gigantic ova and the extension of the mesenteric cord (attaching the ovaries to the body wall) at the level of the anterior fin are evidence that the ovary of *S. enflata* reaches its maximum length in the last reproductive cycle. Taking into account the absence of these characteristics in adults of *S. tasmanica* and that long ovaries were recorded in adult specimens of a wide length range (11 to >19 mm), then we could assume that these individuals reproduce only once per life cycle at the Patagonian shelf.

Ovary length appears to vary according to the area of study. Furnestin (1957) recorded an ovary index of up to 29% (short type) for *S. tasmanica* in Moroccan waters of the Atlantic Ocean. Boltovskoy (1974) reported that the ovaries of *S. tasmanica* individuals reach up to the middle of the anterior fin (short type) in the SWAO (36°S–43°S), in agreement with our results for the NACS. Ghirardelli (1997) observed that *S. tasmanica* individuals distributed from the western (Pacific Ocean) to the eastern entrance (Atlantic Ocean) of the Strait of Magellan had mature ovaries of variable length, sometimes extending beyond the ventral ganglion (long type) in large specimens. Variations in salinity and temperature may lead to morphological differences such as those observed in *Sagitta crassa* (Murakami 1959; Tokioka 1974) and in *S. tasmanica*. Specimens of the latter species from the southeastern Pacific were erroneously assigned by Fagetti (1958) to a new species, *Sagitta selkirki*.

Differences in body length, ovary length and morphology of the seminal vesicles between specimens of *S. tasmanica* from SACS suggest the occurrence of two distinct populations. It is reasonable to assume that some specimens found in this area could have entered the studied region from the Pacific Ocean (across the Strait of Magellan) via a cold water tongue extending northwards along the coast up to ~41°S (Palma and Matano 2012).

Long ovary specimens were not detected at NACS, possibly due to the fact that the Patagonian Current, which transports waters from the Magellan Strait, flows in a NNE direction and leaves the shelf without reaching the northern study area.

Conclusions

In the SWAO, *S. tasmanica* was found on the continental shelf between 34°30' S to 55°S and its

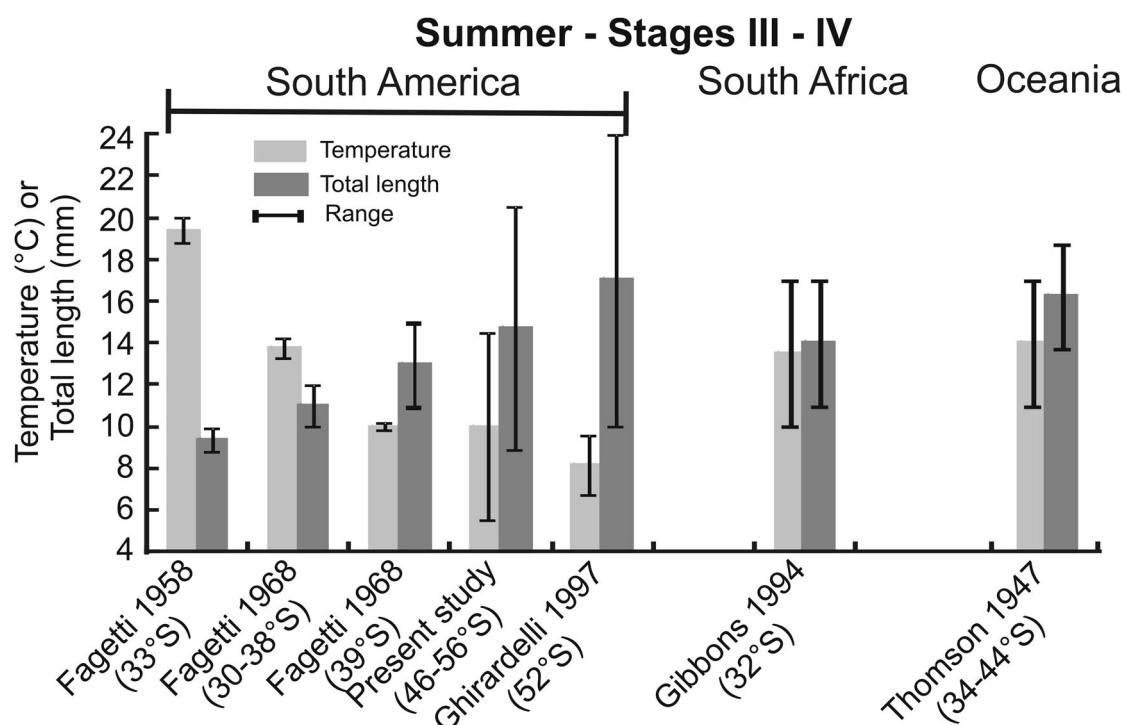


Figure 9. Temperature and total length of adult stages of *Serratosagitta tasmanica* (mean and total range values) from present and previous reports, according to the locations given in Figure 1A.

northward distribution seems to be limited by the Brazil-Malvinas Confluence which is considered a dispersal barrier between warm and cold water organisms. Contrary to the BMC, the Magellan Salinity Front appears to be a less restrictive front allowing the movement of this species to coastal waters. However salinity at both sides of the front may condition the abundance of *S. tasmanica* which showed lower values at salinities up to 32.7 on the west side and higher values at higher salinities on the east side (SASW).

The dominance of this species on the shelf decreased spatially from south to north, whereas biomass increased temporally by three orders of magnitude between spring and summer (12.7 vs 4.06 mgC/m², respectively)

Differences in temperature and salinity found at SWAO would affect not only the distribution of this species but also body length range, its ovary length and the appearance of seminal vesicles. The range of body length was wider for individuals in colder waters than the warmer waters. A higher percentage of individuals with long ovaries was recorded in the SACS area (similar to those individuals from the Magellan Strait and the Southeastern Pacific Ocean). These morphological differences between specimens of *S. tasmanica* from SACS and NACS would suggest the occurrence of two distinct populations.

The presence of all maturity stages and a constant presence of adults from spring to winter, suggests that *S. tasmanica* reproduces all year round in the SWAO. During winter, the high abundance of juveniles and the decline in mature individuals suggest a population turnover.

This is the first study that analyses the distribution, population structure and biomass of *S. tasmanica* in the SWAO, thus contributing to the knowledge of how hydrological processes affect its ecology. Further studies using monthly data collected over one or more years are necessary for a more in-depth understanding of the population dynamics of *S. tasmanica* in the SWAO.

Disclosure statement

No potential conflict of interest was reported by the authors.

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