The influence of environmental conditions on *Parasagitta friderici* (Chaetognatha) abundance in a subtropical estuary (south Brazil)

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Abstract

Estuarine chaetognath population dynamics are poorly known worldwide. We have conducted eight seasonal campaigns (October 2007–August 2008) sampling three sectors in the subtropical Babitonga Bay estuary (26°S 48°W) in order to depict chaetognath abundance and population structure dynamics and test the influence of hydrography and food availability and type. Of three species sampled, *Parasagitta friderici* represented >93% of abundance in all samples and was examined in detail. There were no differences in *P. friderici* abundance between the sectors of the estuary, related to its high tolerance to low salinity, a feature not common for most chaetognath species. Salinity tolerance is an important adaptive characteristic to thrive within estuarine systems, and probably is responsible for the dominance of *P. friderici* in coastal and brackish water environments throughout most of its distribution. Juveniles dominated the population most of the year, except in February–April when abundances were lower and adults predominated. These results suggest that recruitment occurs continuously throughout the year, being more intense between October and January (spring to early summer) and in May (autumn) when densities and proportion of juveniles were higher. General Additive Models suggest that temperature and zooplankton biomass are significant ($P < 0.05$) factors influencing juvenile abundance while only the latter influenced the adults. We conclude that food availability is the most important driver in the studied population of *P. friderici* and recruitment peaks, which lead to high densities, seem to occur following peaks of their copepod prey along with particular temperature conditions (22–23°C).

Introduction

Zooplankton are of great importance in energy transfer and structuring of marine food webs. Thus, detailed descriptions of zooplankton variability and its main drivers are necessary to broaden knowledge of how marine ecosystems function. Chaetognaths are an important planktonic group, commonly present in high densities in marine pelagic environments (Bone *et al.*, 1991; Liang, 2002). They are active predators, grabbing their prey with rigid hooks (Feigenbaum, 1991; Casanova, 1999). Due to their position in the pelagic food web as an intermediate link in the energy flow to higher trophic levels such as fish and ubiquitous occurrence in marine environments, chaetognaths have a key role structuring both coastal and oceanic pelagic communities (Bone *et al.*, 1991; Casanova, 1999).

As typical for most zooplankton taxa (e.g. Boltovskoy, 1999), chaetognaths may be sensitive to changes in the physical structure of the water column, and different hydrographic conditions may lead to different feeding, growth, reproduction and survival rates, influencing their abundance levels and population dynamics (e.g. Ramírez & Viñas, 1982; Daponte *et al.*, 2008; Wu *et al.*, 2014). Apart from the physical environment, biotic factors such as food availability and quality also have an important role influencing chaetognath distribution and population dynamics (Gibbons & Stuart, 1994; Liang *et al.*, 2003; Sato *et al.*, 2011; Noblezada & Campos, 2012). The influence of physical and biological environment on chaetognath populations and their spatial and temporal dynamics from shelf and oceanic ecosystems is relatively well-known, with many available studies on the South-western Atlantic (e.g. Crelier & Daponte, 2004; Araújo & Ribeiro, 2005; Souza *et al.*, 2014) and in most other main regions worldwide (e.g. Gibbons & Stuart, 1994; Nair *et al.*, 2002; Ruiz-Boijseauneau *et al.*, 2004; Noblezada & Campos, 2012; Wu *et al.*, 2014).

In contrast, estuarine chaetognath populations have been poorly studied. Detailed data on abundance, population structure and/or reproduction are available only from a few scattered estuaries and species worldwide (Reeve, 1964; Mulkana & McIlwain, 1973; Grant, 1977; Srinivasan, 1980; Nair & Sankarankutty, 1988; Liang *et al.*, 2003), with even fewer data formally analysing the influence of food availability and hydrographic parameters. Estuaries are typically characterized by a haline horizontal gradient which has a paramount influence on the structure and functioning of communities (Whitfield & Elliott, 2011), including zooplankton abundance, diversity and assemblage structure (Xu *et al.*, 2014; Miyashita & Calliari, 2016). This may be particularly true for chaetognaths since they are exclusively marine

and most species are more common over the continental shelf and offshore (Bone *et al.*, 1991; Casanova, 1999). General latitudinal climatic patterns, reflected mostly by the temperature and rainfall, are expected to influence the seasonal dynamics of estuarine plankton, which typically attain lower abundances during winter in subtropical to temperate latitudes (Reeve, 1964; Marques *et al.*, 2009; Nogueira Júnior *et al.*, 2018), and tend to follow the rainfall regime in tropical regions (Nair, 1974; Hernández *et al.*, 2005). However, the general absence of baseline detailed data hampers broad generalizations and understanding the responses of different species. In the present study we test the role of physical (temperature and salinity) and biological (food availability) factors as drivers of spatial and temporal dynamics of chaetognath population structure through an annual cycle in the subtropical Babitonga Bay estuary, South Brazil.

Materials and methods

Study area

Babitonga Bay estuary is located in the state of Santa Catarina, south Brazil (Figure 1), with an area of ~130 km^2 and average depth of 6 m, and up to 28 m depth in the main canal. The region is characterized by a wet subtropical climate, with mean rainfall of ~2000 mm year^{-1}, a rainy season between spring and late summer/early autumn and a dry season during autumn and winter (DNIT-IME, 2004; Cremer *et al.*, 2006). It has a high biological productivity, sustaining high abundance and diversity of aquatic fauna and flora (Brandini *et al.*, 2006; Vilar *et al.*, 2011; Nogueira Júnior, 2012). Babitonga Bay estuary has a tidal range of ~1.30 m (DNIT-IME, 2004; Cremer *et al.*, 2006). The tide is mixed with semidiurnal dominance and diurnal inequalities with a natural oscillation period of ~3.6 h (Truccolo & Schettini, 1999).

Sampling

Eight seasonal surveys, two in each season, were performed at Babitonga Bay estuary between October 2007 and August 2008. During each field campaign three sectors of the estuary were sampled (Figure 1). In each sector three replicate zooplankton samples were performed with a 40 cm mouth diameter and 200 μm mesh WP-2 plankton net (N = 72), and six replicate samples with a 50 cm mouth diameter and 500 μm mesh WP-2 plankton net (N = 144). Nets were slowly (≤1.5 knots), obliquely hauled for 2–5 min covering most of the water column. Nets were coupled with a mechanical flowmeter (Hydrobios). All hauls (N = 216) were performed during daylight, between 9 a.m. and 3 p.m. Samples were fixed in 4% formaldehyde filtered (<30 μm) seawater solution directly after retrieval of the nets.

Subsurface and near-bottom temperature and salinity were measured with a multi-probe (Horiba U-10) and water transparency with a Secchi disk. Chlorophyll-*a* was estimated based on subsurface samples filtered with Whatman filters (25 mm diameter, GF/F), with pigments extracted in the laboratory (Parsons *et al.*, 1984) and measured on a calibrated fluorometer (Turner Designs – Trilogy).

Whole samples taken with the 200 μm mesh net (N = 72) were analysed under a stereomicroscope (Zeiss, Stemi, 2000) and the chaetognaths were separated, identified (mainly following Casanova, 1999) and quantified. The dominant *Parasagitta friderici* was further classified as either juvenile or adult following standard classification of the species (Boltovskoy, 1975; Mendes *et al.*, 2012). Gelatinous organisms were also manually removed from the samples (Nogueira Júnior, 2012) and the rest of the 200 μm samples were used to estimate zooplankton wet weight (mostly copepods, cladocerans and other crustaceans) by
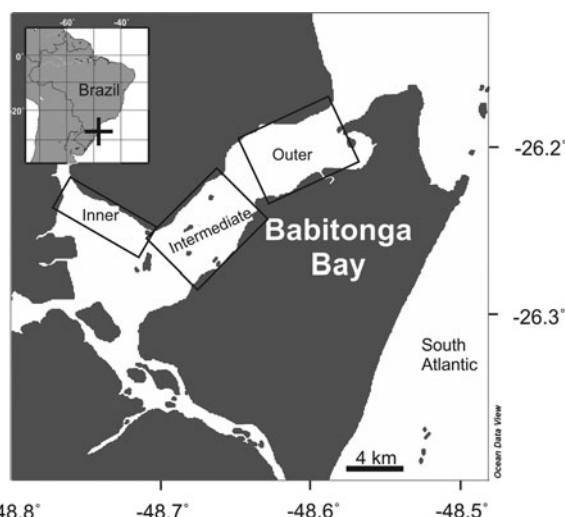

Fig. 1. Map of Babitonga Bay, South Brazil, showing the three sectors sampled between October 2007 and August 2008. Generated using Ocean Data View software (Schlitzer, 2017).

gravimetry after removing the water excess with blotted paper (Omori & Ikeda, 1994), using a digital analytical balance (Lab Genius DL-224) with precision of 0.1 mg. Samples taken with the 500 μm mesh (N = 144) were analysed in their entirety under the stereomicroscope and fish larvae counted. Zooplankton biomass and fish larvae abundance were used to characterize different types of food items and their availability for the chaetognaths.

Data analysis

Two-way analysis of variance (ANOVA) was used to test if the abundance of adult or juvenile *P. friderici* changes significantly ($P < 0.05$) considering temporal (months sampled; eight levels) and spatial (sectors within the estuary; three levels) factors and their interaction (Zar, 2010). To test the effect of different hydrographic and biological variables on juvenile and adult *P. friderici* abundances, we used Generalized Additive Models (GAMs). GAMs are able to deal with non-linear relationships between a dependent variable and multiple predictors in the same model through non-parametric generalizations of multiple linear regressions that are less restrictive about the underlying distribution of data (Hastie & Tibshirani, 1990). Among predictors used, we included physical parameters, such as temperature, salinity and water transparency, and biological parameters such as zooplankton biomass and fish larvae abundance, considered as food source availability for chaetognaths, and chlorophyll-*a* as an indirect measure of biological productivity. Statistical analyses were performed in STATISTICA 13.0.

Results

Abiotic environment

Salinity was always >26 in the outer sector, varying between 26 and 31.5 and between 27.3 and 33.6 in the sub-surface and near the bottom respectively without a clear temporal pattern. In the intermediate and inner sector salinities were lower, ranging in the inner sector from 10.1 to 28.4, and from 16 to 28.8 in the sub-surface and near bottom respectively (Figure 2). While in the outer sector no clear temporal pattern could be discerned, in the intermediate and inner sectors salinity was considerably lower in February (Figure 2), associated with higher rainfall. In February, April, July and August, salinities in the inner and intermediate sectors were similar, while the outer sector salinity was always
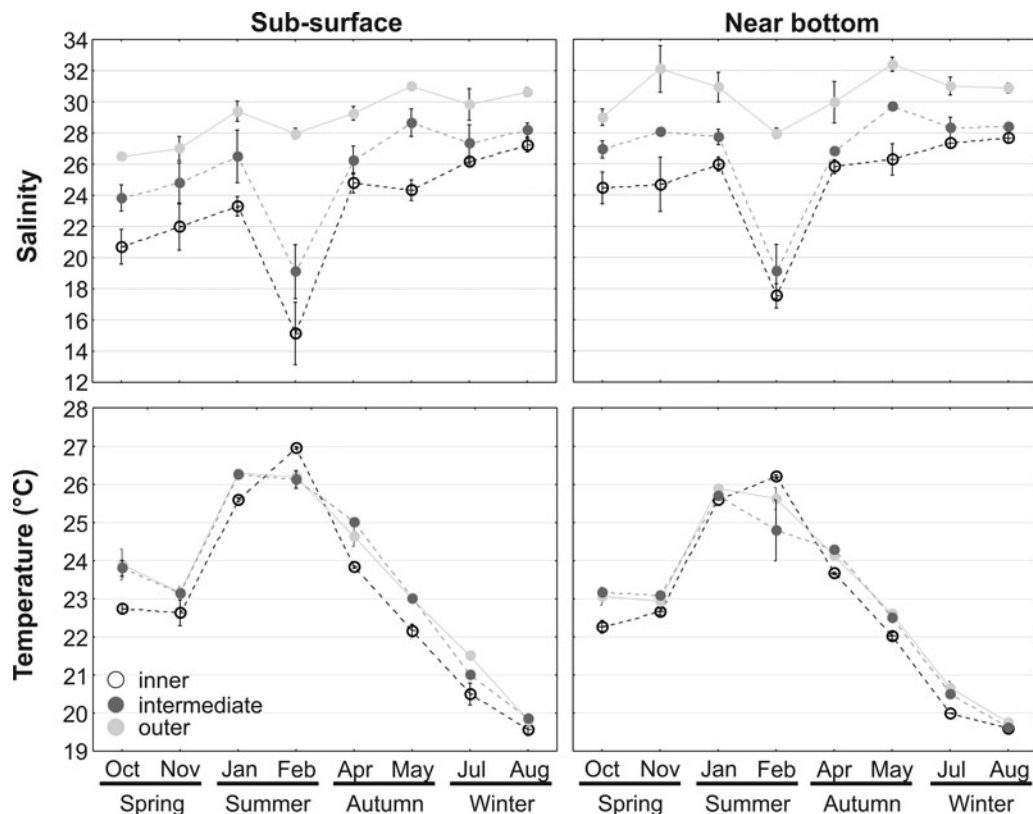
Fig. 2. Abiotic environment. Seasonal variation of sub-surface and near bottom salinity and temperature in the three sectors of Babitonga Bay, South Brazil, between October 2007 and August 2008. Symbols represent the means and vertical bars the standard deviation.

distinct from the other two sectors (Figure 2). Temperature remained between 25–27°C throughout the summer, decreasing to 19.2–19.9°C in August; no spatial differences in the temperature were observed, either horizontally or vertically (Figure 2).

Biotic environment

Two seasonal peaks of chlorophyll-*a* concentration were observed during summer and early winter, tending to be lower in the outer sector particularly during summer (Figure 3A). Zooplankton biomass increased through spring, peaking in January and later decreasing, with a second smaller peak in August in the inner sector (Figure 3C). Fish larvae peaked in November in the outer sector and in January in the intermediate sector. In the inner sector, a peak of fish larvae also occurred in November–January, however, abundances were considerably lower (Figure 3C).

Chaetognaths

Parasagitta friderici, originally described from Cape Verde (Ritter-Záhony, 1911), was always the dominant species in the present study, representing from 93–100% of the chaetognaths from all the samples analysed. Other species found included *Parasagitta tenuis* (Conant, 1896) and *Flaccisagitta enflata* (Grassi, 1881), always in low, intermittent abundances, and exclusively in the outer sector in the case of the latter. *Parasagitta friderici* occurred in all 72 zooplankton samples taken and its abundance ranged from <1 to 250 ind. m^{-3}, averaging (±SD) 36 ± 52 ind. m^{-3}. Juveniles dominated the population throughout most of the year (Figure 4) and represented ~80% of the total annual population, reaching densities of up to 233 ind. m^{-3}. Adults (up to 24 ind. m^{-3}) exceeded juveniles in February and April in all three sectors, representing between 55 and 68% of

total population. In August, adult contribution also was relatively high, particularly in the outer sector, where they represented 49% of the population (Figure 4).

Abundance of both juveniles and adults did not differ between different sectors but differed significantly ($P < 0.05$) through time, considering months, and the interaction between months and sectors (Table 1). This indicates that the spatial distribution was not constant throughout the year. For instance, in October both juveniles and adults were more abundant in the outer sector, while in January and August both tended to be less abundant in this sector (Figure 5A, B). In the inner sector, abundance of juveniles increased through the spring and peaked in early summer (January), when they averaged ~105 ind. m^{-3}. Lower abundances of both juveniles and adults occurred between February and April in all sectors (Figure 5). A second peak of juveniles was observed in May, mostly in the intermediate and outer sectors. In contrast, adult abundances also peaked in August particularly in the inner sector (Figure 5).

The Generalized Additive Model (GAM) explained 69.2% of the deviance in *P. friderici* juvenile abundance. From the six variables considered (temperature, salinity, water transparency, chlorophyll-*a*, zooplankton biomass and fish larvae), the model indicated significant ($P < 0.001$) relationships with zooplankton biomass and sub-surface temperature. For adults, the model explained a lower proportion (45.3%), and suggested a significant ($P < 0.001$) relationship only with zooplankton biomass.

There is a clear tendency of increasing abundance of both juvenile (Figure 6A) and adults (Figure 7) with increasing zooplankton biomass up to around 450 mg m^{-3}. Biomass values above 800 mg m^{-3} were associated mainly with mid-low adult and juvenile densities (Figures 6A & 7) at the inner sector in January (Figure 5A, B). Abundance of juveniles also tended to increase with water temperature, up to 22–23°C, where most of
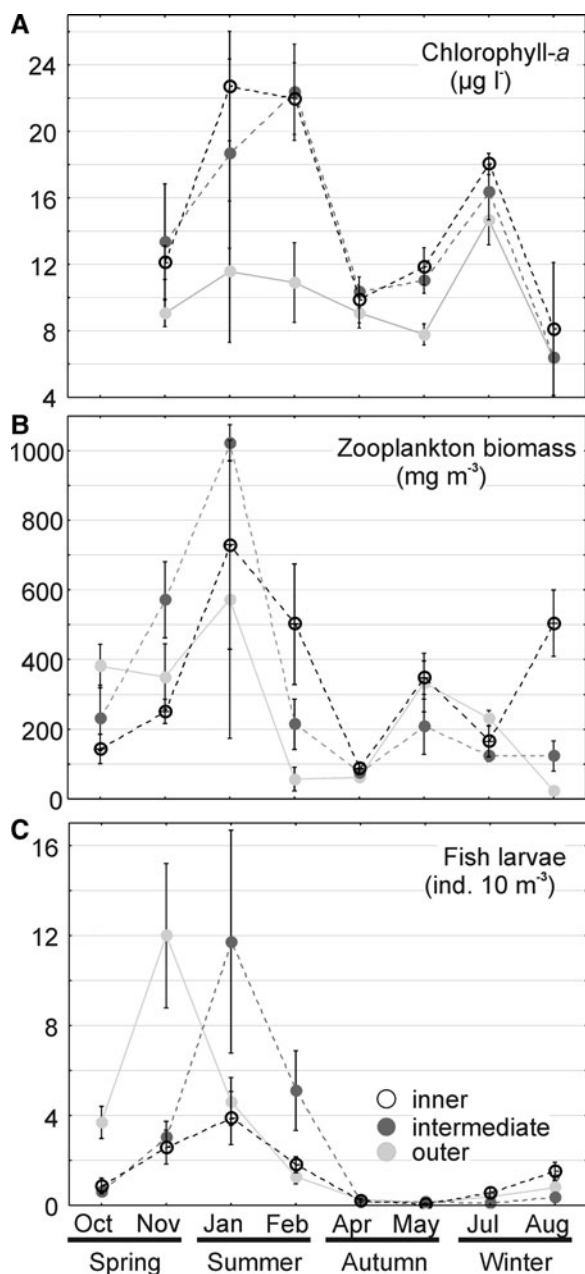
Fig. 4. Seasonal changes in the proportion (% of ind. m^{-3}) of juveniles (grey bars) and adults (black bars) in the three sectors of Babitonga Bay estuary between October 2007 and August 2008.

Fig. 3. Biotic environment. Seasonal variations of chlorophyll-*a* (a), zooplankton biomass (b) and fish larvae abundance (c) in the three sectors of Babitonga Bay estuary, South Brazil, between October 2007 and August 2008. Symbols represent the means and vertical bars the standard deviation.

the high abundances were found (Figure 6B). In warmer waters juvenile abundance tended to decrease, but on a few occasions in January, high juvenile density also occurred with temperatures above 26°C.

Discussion

The high dominance of *P. friderici* observed here is common in South-western Atlantic coastal and estuarine ecosystems, including tropical (0–2°S; Krumme & Liang, 2004; Costa *et al.*, 2008) and subtropical to temperate latitudes (~20–40°S; Boltovskoy, 1975; Loureiro Fernandes *et al.*, 2005; see also references from Table 2). Indeed, this species is amongst the few chaetognaths abundant in and restricted to coastal and neritic waters (Pierrot-Bults & Nair, 1991). It is the dominant species in many coastal and estuarine ecosystems throughout its distribution, such as
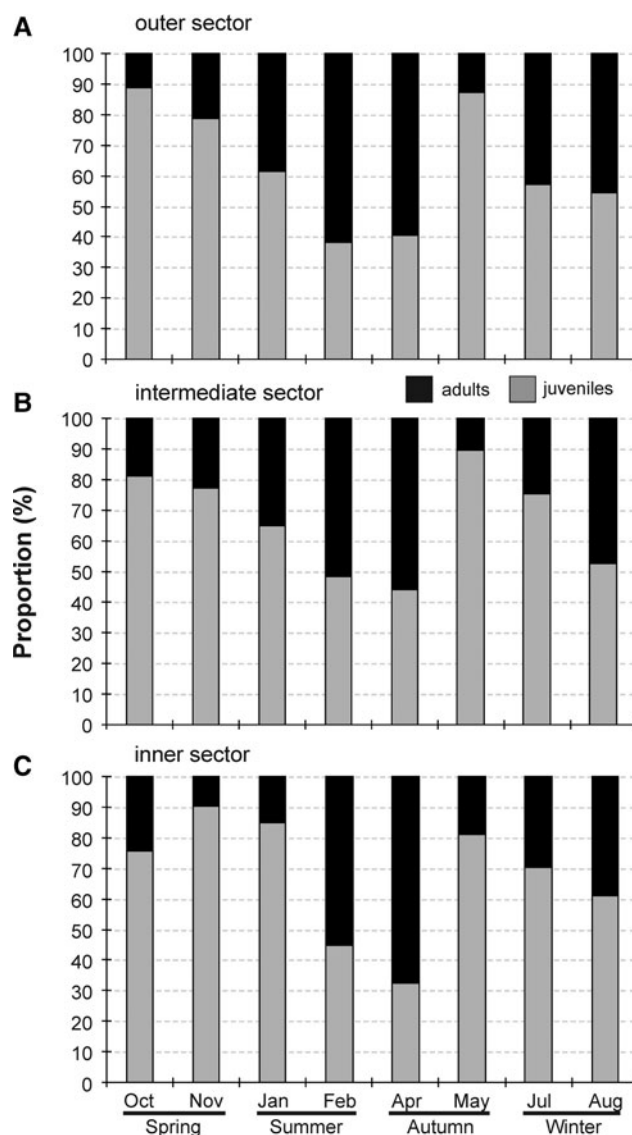
both sides of the North (Furnestin, 1957; Fraser, 1960; McLelland, 1980; Blanco-Bercial *et al.*, 2006; Champalbert *et al.*, 2007; Marques *et al.*, 2009) and South (Stuart & Verheye, 1991; Gibbons & Stuart, 1994) Atlantic up to latitude of ~40°, in the eastern Pacific (Hossfeld, 1996) and the south Mediterranean (Aziz, 2005; Zakaria, 2006).

Densities of *P. friderici* populations found in the South-western Atlantic vary a lot, from <20 ind. m^{-3} in the tropical Caeté River estuary and on the temperate Argentinian Shelf to up to 5746 ind. m^{-3} in the subtropical Santos Bay (Table 2). There is no latitudinal trend in *P. friderici* abundance throughout the South-western Atlantic, with very high densities both in tropical (0.5°S), subtropical (23°50′S) and nearly temperate (31–32°S) latitudes (Table 2). However, near its southernmost limit (>35°S) *P. friderici* abundances are typically low, never exceeding 60 ind. m^{-3} (Table 2), perhaps due to temperature constraints of this warm water species in higher latitudes. The values found here, up to 250 ind. m^{-3} (annual mean of total population = 36 ± 52 ind. m^{-3}) are within this range and, in comparison to other known South-western Atlantic populations (Table 2), cannot be considered either particularly abundant or scarce. Populations of this species elsewhere throughout its distribution also are

Table 1. Summary of the ANOVA testing for differences in abundance of *Parasagitta friderici* juveniles and adults considering months and sectors as factors and their interaction

Maturity stage	Factors	DF	SS	MS	F	P
Juveniles	Month	7	37,870.75	5410.11	3.388	0.004
	Sector	1	1028.37	1028.37	0.644	0.425
	Month × sector	7	32,826.38	4689.48	2.937	0.011
	Residuals	56	89,419.68	1596.78		
Adults	Month	7	1040.58	148.65	6.593	<0.001
	Sector	1	22.24	22.24	0.986	0.325
	Month × sector	7	541.34	77.33	3.430	0.004
	Residuals	56	1262.57	22.55		

DF, degree of freedom; SS, sum of squares; MS, mean squares; F, parameter of the ANOVA; P, probability associated to the test.
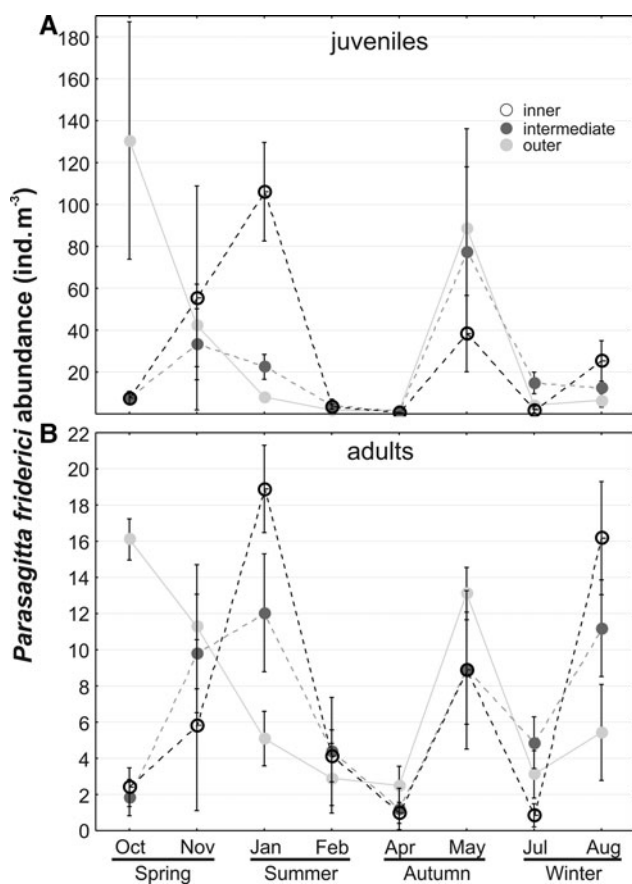Differences are considered significant if $P < 0.05$.

Fig. 5. Seasonal variation of *Parasagitta friderici* juvenile (a) and adult (b) abundance in the three sectors of Babitonga Bay estuary, South Brazil, between October 2007 and August 2008. Symbols represent the means and vertical bars the standard deviation. Notice different scales.

continuously, the year-round occurrence of many juveniles clearly suggests the population is reproducing throughout the year, which is to be expected for tropical and subtropical chaetognaths in general (Ghirardelli, 1968; Ramírez & Viñas, 1982). Even though continuous, reproduction of *P. friderici* was not uniform. Reproductive peaks, as suggested by juvenile peaks, occurred between October and January and in May, as indicated by higher abundances and proportion of juveniles (Figures 4 & 5). In addition, between February and April, and in August, densities were considerably lower and adults represented a larger proportion of the population, suggestive of less intense recruitment in these periods. Although existing data on *P. friderici* are scarce and scattered, they suggest a general trend of continuous reproduction and recruitment with sporadic peaks commonly during spring, as well as higher proportion of adults in late summer and/or early autumn which is probably food-related according to the present data. This pattern includes populations from tropical (Mendes *et al.*, 2012), subtropical (Furnestin, 1957; Liang *et al.*, 2003; this study) and temperate (~38°S; Ramírez & Viñas, 1982; Daponte *et al.*, 2004) latitudes.

The few other studied estuarine chaetognaths worldwide up to ~40° of latitude also have similar patterns of high juvenile dominance suggesting year-round reproduction with intermittent peaks, as is the case for tropical populations of *Zonosagitta bedoti* (Béraneck, 1895), *F. enflata* and *P. tenuis* (Srinivasan, 1980; Nair & Sankarankutty, 1988; Ramaiah & Nair, 1993), subtropical *Ferosagitta hispida* (Conant, 1895) (Reeve, 1964) and temperate *Aidanosagitta regularis* (Aida, 1897) (36°S; Webb & Sewell, 2015). Populations from colder regions such as *Parasagitta setosa* (J. Müller, 1847) from Black Sea (Besiktepe & Unsal, 2000), *Parasagitta elegans* (Verril, 1873) from Charente estuary, France (Modéran *et al.*, 2010) and *P. tenuis* and *F. hispida* from Chesapeake Bay, USA (Grant, 1977) tend to have marked seasonal cycles typically with abundance peaks and high dominance of juveniles mostly during summer, or occasionally winter such as *P. elegans* from Chesapeake Bay (Grant, 1977).

The presence of *P. friderici* throughout the salinity range sampled in the present study, from 10.1 to 33.6, is not surprising considering that this chaetognath is known to commonly dwell in both lower and higher salinities (Furnestin, 1957; Liang *et al.*, 2003; Blanco-Bercial *et al.*, 2006; Cervetto *et al.*, 2006). Consequently, salinity did not significantly explain part of either adult or juvenile abundance variations in the present study according to the GAM, supporting the hypothesis that salinity variations are not of great importance for this species (Fraser, 1960). This high tolerance of *P. friderici* to salinity variations is an important adaptation to thrive within estuarine systems and

within this abundance range (Stuart & Verheye, 1991; Gibbons & Stuart, 1994; Hossfeld, 1996; Champalbert *et al.*, 2007; Marques *et al.*, 2009), as are other estuarine and coastal chaetognaths worldwide (Reeve, 1964; Srinivasan, 1971; Nair, 1974; Grant, 1977; Nair *et al.*, 1981; Besiktepe & Unsal, 2000; Hernández *et al.*, 2005; Modéran *et al.*, 2010; Noblezada & Campos, 2012; Wu *et al.*, 2014).

The constant and abundant presence of juveniles throughout the year indicates continuous reproduction and recruitment. Although we did not evaluate in detail reproduction in the present study, and not necessarily all adult individuals are reproducing

Fig. 6. Results of the Generalized Additive Model for *Parasagitta friderici* juveniles showing the abundance trends and the effect modelled of zooplankton biomass (a) and sub-surface temperature (b). Solid lines show the smoothing function and dotted lines the 95% confidence interval.
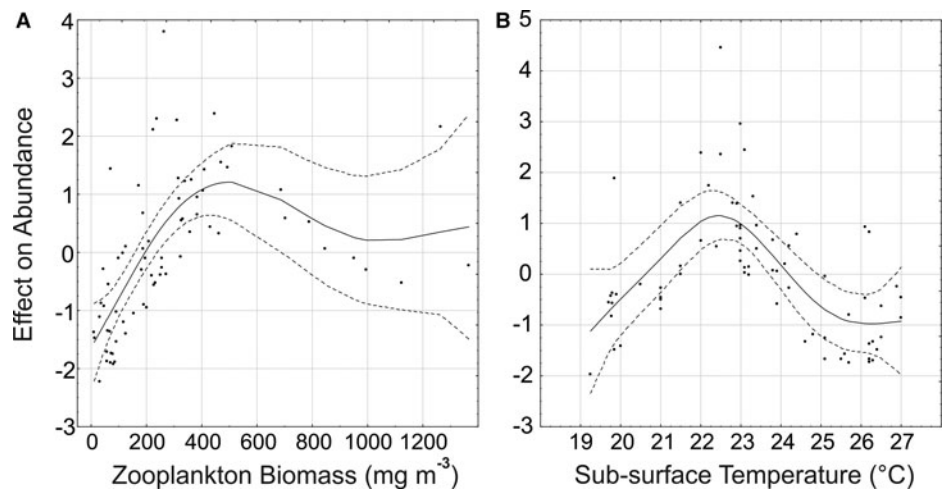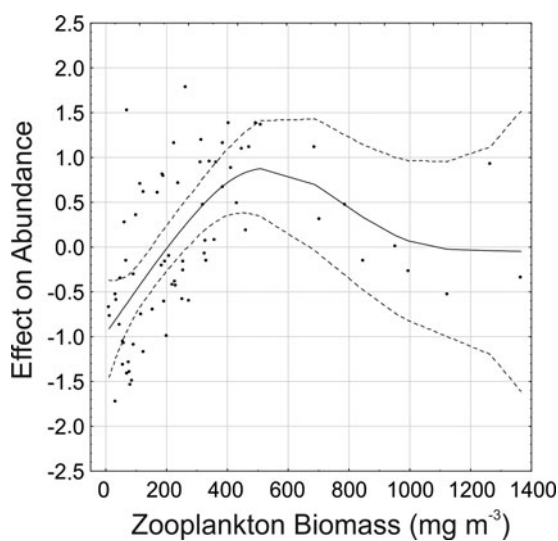

Fig. 7. Result of the Generalized Additive Model for *Parasagitta friderici* adults showing the abundance trends and the effect modelled of zooplankton biomass. Solid lines show the smoothing function and dotted lines the 95% confidence interval.

is different to most other chaetognath species worldwide which are commonly highly influenced by this factor (e.g. Srinivasan, 1971; Nair, 1974; Grant, 1977; Blanco-Bercial *et al.*, 2006). Moreover, since salinity commonly is the main factor affecting spatial structure of estuarine zooplankton in general (e.g. Xu *et al.*, 2014; Miyashita & Calliari, 2016) and of chaetognaths in particular (Srinivasan, 1971, 1980; Nair, 1974; Loureiro Fernandes *et al.*, 2005), this high tolerance of *P. friderici* probably accounts for the similar densities of both juvenile and adults in all three sectors sampled. Hitherto, laboratory survival experiments have not been performed and are necessary to determine the extent of *P. friderici* resistance and the effects of reduced salinity on its biological parameters such as feeding, growth and reproductive output.

Most environmental variables tested in the present study were not significantly related to either juvenile or adult abundance according to the GAM analyses. Zooplankton biomass was the best predictor of both adults and juveniles, along with temperature for the latter category. Accordingly, *P. friderici* is known to occur in a wide range of hydrographic conditions, wider than the ones found here for both salinity (see above) and temperature. This species is known to grow and reproduce in 10°C waters (Daponte *et al.*, 2004), considerably colder than the minimum recorded here (19.2°C). Thus, these hydrographic parameters

probably are not major limiting factors for *P. friderici* populations in the subtropical Babitonga estuary. The relationship of juveniles with temperature probably is due to the thermal influence on reproduction, development and growth rates of chaetognaths in general (Russell, 1932; Ghirardelli, 1968; Terazaki, 2004) and *P. friderici* in particular (Ramírez & Viñas, 1982; Resgalla, 2010). According to our results, the optimal temperature range for juveniles is 22–23°C (Figure 6B). This agrees with the negative relationship between *P. friderici* and temperature in a tropical estuary with annual temperature range between 22 and 29°C (Loureiro Fernandes *et al.*, 2005), and with the positive relationship with temperature in temperate areas (Blanco-Bercial *et al.*, 2006). The difference in environmental preferences between juveniles and adults is similar to the related species *Parasagitta setosa* from the Black Sea where adults tolerate a wider temperature range than juveniles (Besiktepe and Unsal, 2000), resulting in the higher influence of temperature on juveniles as observed here.

The observed relationship of both juveniles and adults with zooplankton biomass is probably trophic-related. All gelatinous and semi-gelatinous organisms were removed from the samples, prior to weighing, and so the bulk of the biomass estimated here was composed of crustaceans, particularly the copepods *Acartia tonsa* Dana, 1849, *Acartia lilljeborgi* Giesbrecht, 1889, *Temora turbinata* (Dana, 1849), *Oithona hebes* Giesbrecht, 1891 and *Pseudodiaptomus acutus* (Dahl F., 1894) (Souza, 2013). These copepod taxa are amongst the main prey items of *P. friderici*, although other zooplankton such as appendicularians, molluscs, cladocerans and chaetognaths may also be eaten (Stuart & Verheye, 1991; Vega-Pérez & Liang, 1992; Liang & Vega-Pérez, 1995; Liang *et al.*, 2003; Sato *et al.*, 2011). Chaetognaths may prey on a variety of planktonic organisms but their diet is typically composed mainly of copepods, reflecting the general composition of the zooplanktonic community (Feigenbaum, 1991; Casanova, 1999). Although chaetognaths may impact fish larvae abundance (Casanova, 1999), predation on ichthyoplankton is usually smaller (Feigenbaum, 1991). Accordingly, *P. friderici* distribution was not explained by fish larvae abundance in the present study. Food availability has commonly been considered an important factor controlling spatial and seasonal patterns of chaetognath abundance and reproduction both on estuarine and open shelf water ecosystems (Bone *et al.*, 1991; Gibbons & Stuart, 1994; Liang, 2002; Terazaki, 2004; Loureiro Fernandes *et al.*, 2005; Noblezada & Campos, 2012). This may be particularly true for *P. friderici* (e.g. Liang *et al.*, 2003) which has a wide tolerance for hydrographic conditions (see above) and thus food availability and quality appears as the main driver of its spatial and temporal dynamics as suggested here.

Table 2. Comparison of mean and maximum abundance (ind. m^{-3}) of *Parasagitta friderici* from several South-western Atlantic estuarine and open shallow shelf waters

Location	Mean abundance ± SD	Maximum abundance	Mesh size (μm)	Data source
Taperaçu Estuary (0°55′S)	848 ± 1050	>1400[a]	120	Costa *et al.* (2008)
Caeté River Estuary (0°50′S)	2.11	18	300	Krumme & Liang (2004)
Vitória Bay (20°S)		36	200	Loureiro-Fernandes *et al.* (2005)
Ribeira Bay (23°S)	35.7	383	150	Dias & Bonecker (2008)
Guanabara Bay (23°S)	9.5 ± 19.9	101	200	Marazzo & Nogueira (1996)
Guanabara Bay (23°S)		560	200	Mendes *et al.* (2012)
Santos Bay (23°50′S)		5746	140	Pereira (2011)
Cananéia Lagoon (24–25°S)		373	150	Liang *et al.* (2003)
São Paulo coast (25°S)		~200	58 meshes/inch (200–300 μm)	Almeida Prado (1968)
Paranaguá estuarine system (25.5°S)	1.2	48.7	300	Miyashita *et al.* (2012)
Babitonga Bay (26°S)	36 ± 52	250	200	this study
Patos lagoon (31°50′S/52°2′W)	430	1373	200	Montú (1980)
Cassino Beach (32°S)	158	1398	300	Resgalla (2010)
Argentinian Shelf (35–39°S)		20	400	Daponte *et al.* (2011)
Off Rio de la Plata (~34–37°S)	22	541	220	Viñas *et al.* (2002)
Mar del Plata coast (38°S)		57	200	Daponte *et al.* (2004, 2008)
El Rincón (39–41°S)		40	Na	Daponte *et al.* (2006)

SD, standard deviation.

[a]The authors only mention mean abundance and thus we provided a conservative estimation of maximum abundances of >1400 ind. m^{-3}.

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