COMPOSITION, DENSITY, AND BIOMASS OF SALPIDAE AND CHAETOGNATHA IN THE SOUTHWESTERN ATLANTIC OCEAN (34.5°S–39°S)

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ABSTRACT

Salps and chaetognaths constitute an important fraction of the macrozooplankton and have a prominent role in the marine food web. In our study, we analyzed the species composition, density, and biomass in an area of the southern Atlantic Ocean during the austral winters of 1999, 2000, and 2001. The most abundant and frequent species were the salpids *Ihlea magalhanica* (Apstein, 1894) and *Iasis zonaria* (Pallas, 1774), and the chaetognaths *Parasagitta friderici* (Ritter-Záhony, 1911) and *Serratosagitta tasmanica* (Thomson, 1947). Chaetognaths were found in over 80% of the stations throughout the three winters, reaching up to 67 individuals (ind) m^{-3}. Salps were found surviving at low population densities in 2000 and 2001, but in 1999, there were mass occurrences of *I. zonaria* and *I. magalhanica*, reaching densities of 301 and 123 ind m^{-3}, respectively. To estimate biomass in C units, the relationship between dry weight and size was calculated for *S. tasmanica* and for solitaries and aggregates of *I. zonaria* and *I. magalhanica*. The biomass of salps and chaetognaths (as mg C m^{-3}) over the shelf during the three consecutive winters was strongly related to prevailing physical and biological conditions. In 1999, the greatest contribution to macrozooplankton biomass corresponded to salps, while in 2000 and 2001, chaetognaths dominated the biomass. In swarm conditions, like in 1999, *I. zonaria* and *I. magalhanica* widely dominated over copepods and chaetognaths, producing an increase in the quantity of available C of up to 60 times in relation to the periods with very low population densities.

Salps and chaetognaths constitute an important fraction of the macrozooplankton and have a prominent role in the marine food web. However, much remains to be learned about their role in the neritic sector of the southwestern Atlantic Ocean. In this area, not only have studies been qualitative rather than quantitative (Esnal and Daponte 1999), but research on abundance (biomass, density) has also been rare (e.g., Daponte et al. 1993, Crelier and Daponte 2004, Loureiro-Fernandes et al. 2005).

Since salps are very efficient grazers that can retain particles from < 1 μm to 1 mm (Madin 1974, Kremer and Madin 1992, Madin and Purcell 1992) and carnivorous chaetognaths prey on different groups of invertebrates, both taxa affect the ecosystem in different ways. In the life history of salps, there are two different generations: oozooids (solitaries) and blastozooids (aggregates). The blastozooids reproduce sexually, giving rise to oozooids. The oozooids, in turn, reproduce asexually, producing a variable number of blastozooids that, in a favorable feeding environment, can form dense swarms covering large areas for several months (Andersen 1998). These outbreaks are clearly the result of the interactions between the biology of the animal and the physical environment (Graham et al. 2001). Most

of the recorded outbreaks have been produced by a small number of species, such as *Thalia democratica* (Forskål, 1775) (e.g., Heron and Benham 1984, Paffenhöfer et al. 1995, Zeldis et al. 1995, Deibel and Paffenhöfer 2009), *Salpa aspera* Chamiso, 1819 (e.g., Wiebe et al. 1979, Madin et al. 2006), *Salpa fusiformis* Cuvier, 1804 (e.g., Yount 1958, Fraser 1969), and *Salpa thompsoni* Foxton, 1961 (e.g., Siegel and Loeb 1995, Perissinotto and Pakhomov 1998, Chiba et al. 1999). During these mass occurrences of salps, their grazing pressure exerts an intense effect on phytoplankton (Zeldis et al. 1995) and microzooplankton (Vargas and Madin 2004), hence they can substantially modify the epipelagic food web (Landry and Calbet 2004). Furthermore, through their fecal pellets, salp swarms contribute to the export of a significant amount of organic matter from the euphotic zone to deeper layers (Bathmann 1988, Madin et al. 2006), consequently participating in the sequestration of atmospheric greenhouse gases (Karl et al. 2001).

Chaetognaths are conspicuous predators in both oceanic and coastal areas (Alvariño 1965, Dilling and Alldredge 1993), frequently ranking second after copepods (Froneman et al. 1998). During their life cycle, they feed mainly on copepods (Feigenbaum and Maris 1984), but also on larvae and adults of various planktonic invertebrates (Baier and Purcell 1997, Marazzo et al. 1997, Froneman et al. 1998), as well as on fish larvae (Alvariño 1985, Baier and Purcell 1997). Due to the large abundance of chaetognaths and the fact that they consume the same food usually consumed by fish larvae (e.g., copepods, appendicularians, mollusk larvae), chaetognaths may affect fish populations by food competition (Baier and Purcell 1997, Coston-Clements et al. 2009). In addition to the trophic role played by salps and chaetognaths in the marine food web, they also comprise important food items for a number of predators, including several fish species that feed on salps (Kashkina 1986, Morato et al. 2000, Mianzan et al. 2001, Szedlmayer and Lee 2004) and/or chaetognaths (Cavalieri 1963, Terazaki and Iwata 1982, Brodeur et al. 2000, Sardiña and Lopez Cazorla 2005, Terazaki 2005).

The neritic sector of the southwestern Atlantic Ocean contains several frontal zones (Acha et al. 2004) characterized by high chlorophyll-*a* (Chl-*a*) (Podestá 1997) and herbivorous zooplankton biomass (Mianzan et al. 2001, Sabatini and Alvarez Colombo 2001). These conditions favor the presence of predators such as fishes (Ehrlich 2000, Sánchez and Ciechomski 1995), pelagic seabirds (Schiavini et al. 1998), and seals (Campagna et al. 1998), which are attracted by the high food availability. The area between 34°S and 39°30′S (Fig. 1) is the northern sector of the Argentinean Continental Shelf, characterized as a complex oceanographic and ecological system (Lucas et al. 2005), which is influenced by the presence of warm-high salinity waters from the Brazil Current, cold-low salinity waters from Malvinas currents, and freshwater runoff from Rio de la Plata. Recent studies show marked variations in Chl-*a* distribution throughout the year, with a phytoplankton bloom in early spring and a smaller bloom in early fall (Lutz et al. 2006). Zooplankton also exhibit two abundance periods, one in winter and another in spring–summer, just after the phytoplankton peaks (Viñas et al. 2011).

The whole sector is a spawning and feeding ground of commercially important fishes (Boschi 1988, Acha et al. 2004, Machinandiarena et al. 2006), and some of these species feed primarily on zooplankton (Angelescu 1982, Viñas and Ramirez 1996), including salps (Mianzan et al. 1997) and chaetognaths (Cavalieri 1963). For instance, the coastal zone is the spawning and nursery ground of white croaker,

Micropogonias furnieri Desmarest, 1823, the striped weakfish, *Cynoscion striatus* (Cuvier, 1829), parona leatherjack, *Parona signata* (Jenyns, 1841), and several species of shrimp. The shelf waters are the spawning and nursery area of mackerel, *Scomber japonicus* Houttuyn, 1782, argentine hake, *Merluccius hubbsi* Marini, 1933, and anchovy, *Engraulis anchoita* Hubbs and Marini, 1935.

Although the area has been subject of many studies related to hydrography (e.g., Pereira Brandini et al. 2000, Muelbert et al. 2008, Piola et al. 2008), copepods (Berasategui et al. 2006, Marrari et al. 2004, Viñas et al. 2002), ichthyoplankton (Hoffmeyer et al. 2009, Machinandiarena et al. 2006), and fisheries (Macchi 1998, Bezzi et al. 2000), little attention has been paid to gelatinous and semigelatinous zooplankton, thus several aspects of their distribution and biology are not well known compared to those of many crustacean groups. The main objective of our study was to improve the information available on the ecology of salps and chaetognaths in the northern sector of the Argentinean continental shelf. We investigated the most frequently occuring species in the area to examine differences in their distribution, density, and biomass over three consecutive winters.

Material and Methods

Physical Description of the Study Area.—The water masses of the continental shelf between 34°S and 39°30′S (Fig. 1) are the result of the mixing of open ocean waters of the western boundary currents of the South Atlantic Ocean with local sources of continental run-off (Lusquiños and Valdéz 1971). The open ocean circulation is dominated by the opposing flows of the Brazil (subtropical) and the Malvinas (subantarctic) Currents. Both currents meet, on average, at 36°S (Olson et al. 1988). In this area, referred to as the Brazil/Malvinas Confluence, the two flows turn offshore in a series of large amplitude meanders. The geographical location of the front may vary according to the dynamics of the Malvinas Current, for which cyclical variations have been reported (Olson et al. 1988, Fedulov et al. 1990).

In the middle continental shelf, the cold-fresh Subantarctic Shelf Waters (SASW, derived from the Patagonia continental shelf) dominate south of ~33°S, while the warm-salty Subtropical Shelf Waters (STSW), which are primarily influenced by subtropical waters derived from the Brazil Current, extend north of that latitude (Piola et al. 2000). A sharp thermocline transition between SASW and STSW reflects the mixing between these water masses. The Subtropical Shelf Front (STSF) appears to be an extension over the continental shelf of the subantarctic–subtropical transition observed at the Brazil/Malvinas Confluence (Piola et al. 2000). This STSF is located near the 50 m isobath at 32°S and extends to the south toward the shelf break.

A major river discharge on this area corresponds to the Rio de la Plata (Fig. 1), which drains the second largest watershed in South America, discharging an average of 22,000 $m^3 s^{-1}$ to 30,000 $m^3 s^{-1}$ (Urien 1972, Framiñan and Brown 1996). The system is characterized by a strong vertical stratification: fresh water flows seaward on the surface while denser shelf water intrudes along the bottom, taking the shape of a salt wedge.

Sample Collection.—Gelatinous and semigelatinous zooplankton were sampled during several cruises to collect ichthyoplankton by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Argentina. Oceanographic sampling in the area was conducted along eight major transects, T1–T8, oriented perpendicularly to the major water masses (SASW–STSW), from shallow waters to the shelf break (200 m isobath). Each transect included three to eight stations (some beyond the continental slope), 10 nmi apart (Fig. 1).

Plankton samples were collected aboard the RV Holmberg and Oca Balda during the austral winters of 1999 (June 5–13), 2000 (July 20–31), and 2001 (June 30–July 10) with a
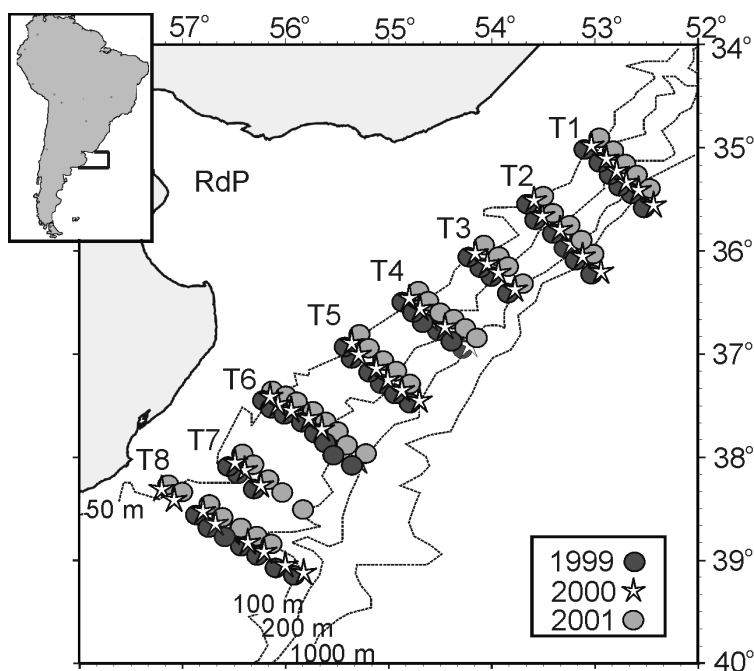
Figure 1. Sampling area and station locations along transects 1–8 (T1–T8) in June 1999, July 2000, and July 2001. RdP: Rio de la Plata.

Nackthai sampler (Nellen and Hempel 1969), with a mouth diameter of 20 cm, fitted with a 400-µm mesh net, equipped with a Hydro-bios flowmeter, and towed obliquely from 5 m above the bottom to the surface. Although Nackthai is not the most desirable sampler for the collection of gelatinous zooplankton, when the tow speed was reduced to 3 kts, the material was obtained in very good condition. Possible errors, such as net avoidance by chaetognaths, should have similar effects along all the years sampled. Oceanographic data were obtained with a Sea-Bird 19 Conductivity-Temperature-Depth (CTD) profiler, calibrated with salinity measurements made with a Guildline "Autosal." Further data processing was performed with standard Seasoft© (Sea-Bird Electronics 1997) routines from which temperature and salinity values with a vertical resolution of 1 db were obtained. Chl-*a* data were obtained from Sea-WiFS imagery monthly composite (http://oceancolor.gsfc.nasa.gov/imagery) corresponding to June 1999, and July 2000 and 2001. Biological samples were preserved in buffered formaldehyde (2%) in seawater.

Only salps and chaetognaths were examined in our study. For each sample, all of the individuals belonging to these two groups were sorted out and each specimen was identified to the species level, with chaetognaths following Bieri (1991) and salps according to Esnal and Daponte (1999). In addition, the total number of copepods in each sample was counted, and abundance levels were expressed as individuals (ind) per m³.

SIZE VS DRY WEIGHT RELATIONSHIP AND BIOMASS ESTIMATION.—Total length (TL) of each salp and chaetognath specimen was measured to the nearest mm. Chaetognaths were measured from the top of the head to the end of the tail (excluding the caudal fin). Salp oozooids and blastozooids were measured from the oral to the atrial siphon. Dry weight (DW) was estimated from TL based on known relationships. DW of the chaetognath *Serratosagitta tasmanica* (Thomson, 1947) and the salps *Iasis zonaria* (Pallas, 1774) and *Ihlea magalhanica* (Apstein, 1874) were estimated according to Lovegrove (1966). The specimens were selected from samples from different stations so as to encompass the range of sizes in each species.

Each specimen was washed in distilled water for 3–4 s, rolled over filter paper, placed in pre-weighted aluminum-foil containers, and oven-dried at 60 °C for 24 hrs (48 hrs for *I. zonaria*). Dry specimens were kept in a desiccator until they cooled down, and then were weighed on a 1 μg-precision microanalytic balance (Sartorius MP1000) or an analytical balance (1 mg-precision) in the case of *I. zonaria*.

We selected a total of 100 ind of *S. tasmanica* ranking between 6.4 and 17.4 mm, well preserved, and without parasites or food residues inside. The specimens were grouped in 17 size intervals of 0.7 mm each. The number of chaetognaths in each interval varied from 2 to 10. The TL–DW relationship for *Parasagitta friderici* (Ritter-Záhony, 1911) was DW: 2.96 log TL – 1.02 (Daponte et al. 2004).

The DW of salp oozooids and blastozooids was determined separately. Selected *I. zonaria* blastozooids (n = 96), ranging between 4.0 and 42.0 mm, were grouped in 19 intervals of 2 mm each. Oozooids (n = 52), ranging between 32.0 and 88.0 mm, were grouped in 3-mm intervals. The size range considered for *I. magalhanica* was 2.0–18.0 mm for blastozooids (n = 85) and 2.3–30 mm for oozooids (n = 159), and each was grouped into 2-mm intervals.

The amount of C (as % of DW) present in salps was estimated by averaging the values reported for different species by Andersen (1998) as: C = 7.76 as %DW. In the case of chaetognaths, this estimation was done according to the values obtained by Conway and Robins (1991): 33.5 ± 5.4 as %DW for *Parasagitta elegans* (Verrill, 1873) specimens fixed with borax buffered formaldehyde in seawater. The biomass of each group was expressed as mg C m^{-3}.

We have made no attempt to correct for the shrinkage of specimens in preservation; therefore, biomass of fresh specimens may be higher than our estimations based on preserved specimens, but should be consistent among the 3 yrs analyzed.

Statistical Analysis.—The data were log transformed ($y' = \ln y$). For the biomass (measured as mg C m^{-3}) analysis, a repeated measures design was used where the factor was the transect, with eight levels, and the repeated measures were the years, with three levels: 1999, 2000, and 2001. The latter year was only considered for chaetognaths, because the presence of salps was only occasional. When necessary, Tukey comparisons (Sokal and Rolhf 1995) were done. Due to the fact that the design requires balanced data and that the 2001 cruise only had four samples in T3, four stations were selected randomly in each transect belonging to each year and the analysis was performed with these data.

The correlations between density (ind m^{-3}) of salps and chaetognaths with abundance of copepods, temperature, and salinity (as integrated values from sampling depth to surface) and surface Chl-*a* for all winters were studied using the Pearson correlation index. Finally, we regressed DW as a function of size for oozooids and blastozooids of *I. zonaria* and *I. magalhanica* and their slopes were compared.

Results

Distribution of Physicochemical Parameters.—The distribution of surface Chl-*a*, temperature, and salinity differed between all three sampling periods (Table 1) and were related to variations in the presence of the major water masses. In June 1999, the maximum surface temperatures occurred over the coastal area (13.0 °C) and in offshore waters of T1. A gradient between 8.0 and 13.0 °C (Fig. 2A) was observed over the middle shelf. Similarly, higher surface salinity (34.2) was found toward T1 in offshore waters and lower salinities in coastal waters of T2 (32.4) and T6 (33.2). In addition, the vertical distribution of temperature and salinity varied with the latitude. Along T1, for instance, homogenous waters were observed over the shelf (temperature ranged from 10.0 to 11.0 °C and salinity from 33.8 to 33.9), while warmer waters and higher salinities were found offshore between 0 and 150 m depth (temperature ranged from 12.0 to 13.0 °C and salinity from 34.0 to 34.9; Fig. 3A,B) as

a result of the mixing between shelf water and STSW. On T5, temperature fluctuated between 12.0 and 10.0 °C near the mouth of the Rio de la Plata from 0 to 50 m and from 9.0 to 6.0 °C below 50 m toward the continental slope (Fig. 3C). The salinity was homogenous along the shelf (33.8–33.9) from 0 to 150 m (Fig. 3D). Consequently, the observed ranges in temperature and salinity indicate the presence of SASW in most of the middle shelf as well as the presence of coastal waters mixed with both low salinity waters from the Rio de La Plata and STSW waters in the offshore waters of T1.

Table 1. Maximum (max) and minimum (min) values for surface temperature (°C), salinity, and chlorophyll-*a* (mg Chl-*a* m^{-3}) recorded in 1999 (June 5–13), 2000 (July 20–31), and 2001 (June 30–July 10). Chl-*a* distribution is expressed as percentage of stations with values between 0.3 and 1.0 mg m^{-3}.

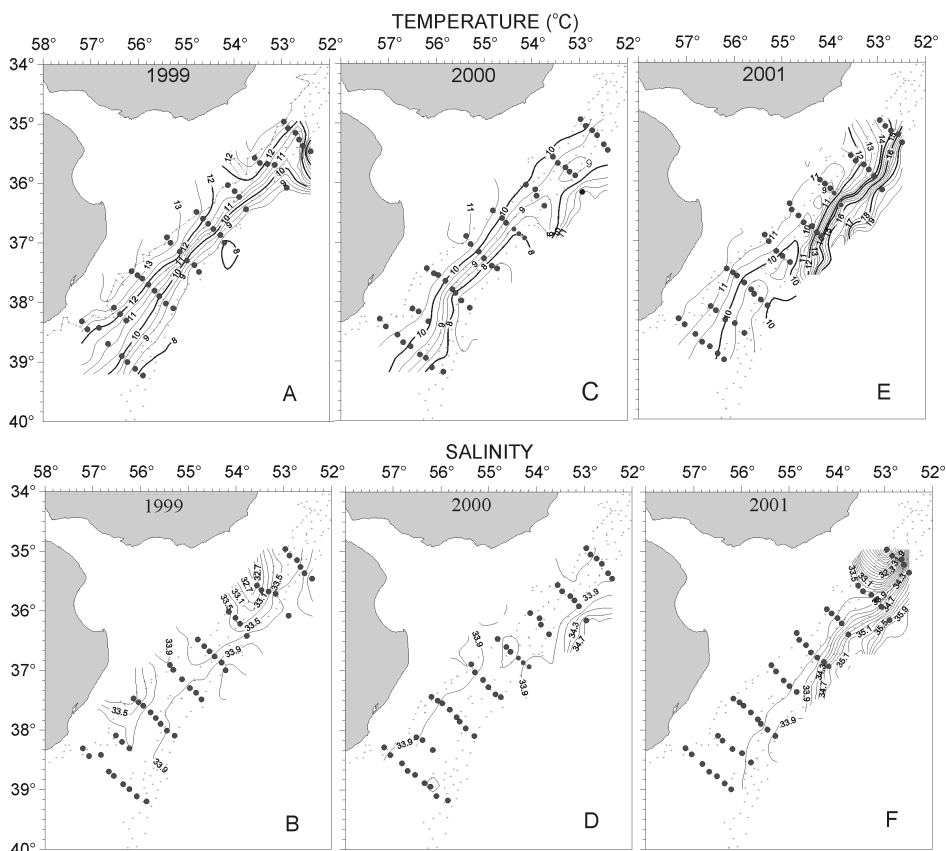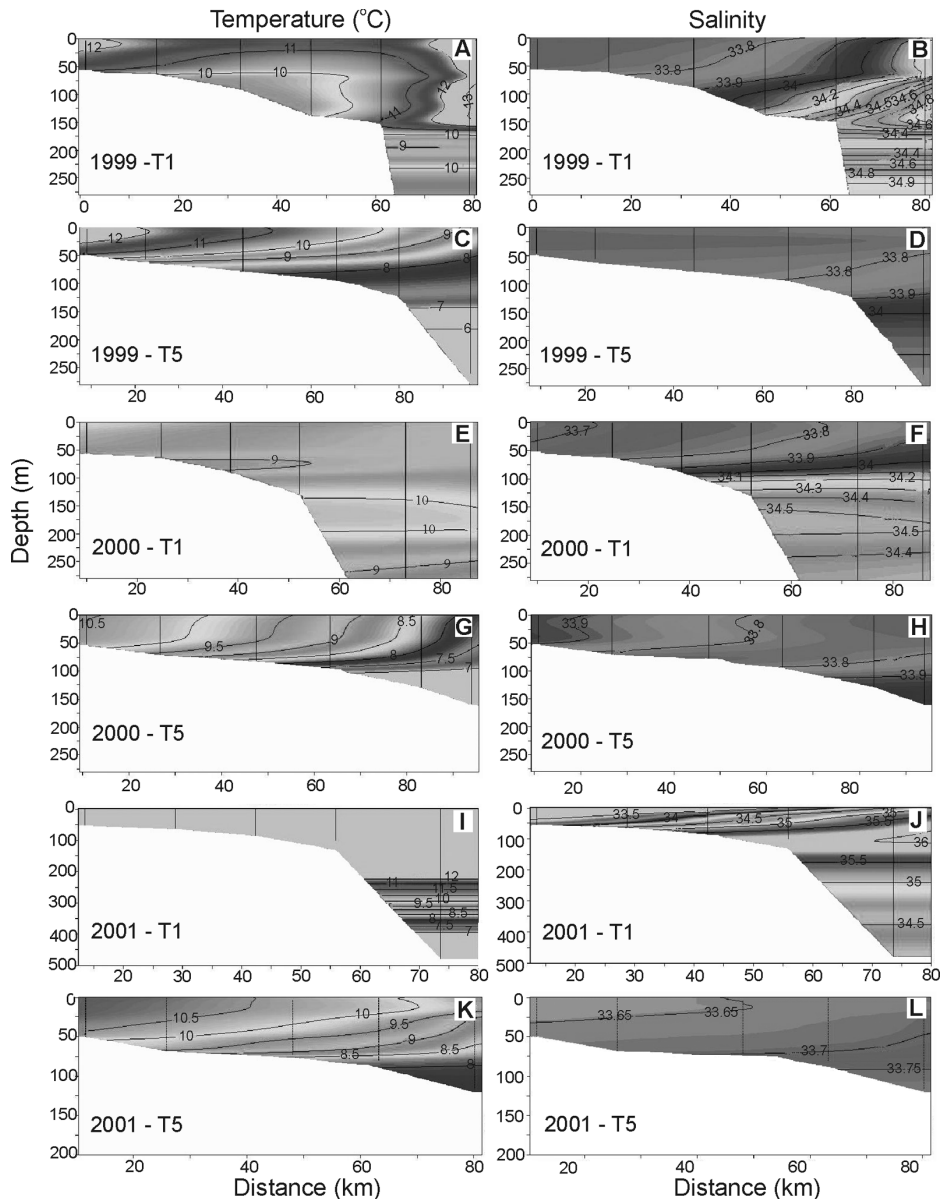| Year	Temperature (°C)		Salinity		Chlorophyll-*a* (mg m^{-3})		
	Min	Max	Min	Max	Min	Max	Distribution
1999	8.0	13.0	32.4	34.2	0.3	2.5	52.5%
2000	7.5	10.5	33.9	34.7	0.3	2.5	42.0%
2001	9.0	19.6	29.7	35.9	0.3	2.5	39.0%

TEMPERATURE (°C)

SALINITY

Figure 2. Surface temperature and salinity distribution in (A–B) 1999, (C–D) 2000, and (E–F) 2001 in the sampling area off the Rio de la Plata.

In 2000, the temperature distribution was similar to that observed in 1999, with relative maxima over deep waters of the northern transect. The shelf temperature was the lowest among the three years studied and decreased from the coast toward the continental slope. The surface maximum horizontal gradient, 7.5–10.5 °C, was mainly situated between the latitudes 39.5°S and 36.5°S (Fig. 2C). Over the middle shelf, the salinity was homogeneous with values between 33.9 (indicative of SASW waters) and 34.7 (Fig. 2D). Regarding vertical distribution, temperature varied from 9.0 to 10.0 °C from 0 to 125 m depth (Fig. 3E) and salinity reached 34.4 in the deep

Figure 3. Vertical distribution of temperature (°C) and salinity in transects 1 (T1) and 5 (T5) in (A–D) June 1999, (E–H) July 2000, and (I–L) July 2001.
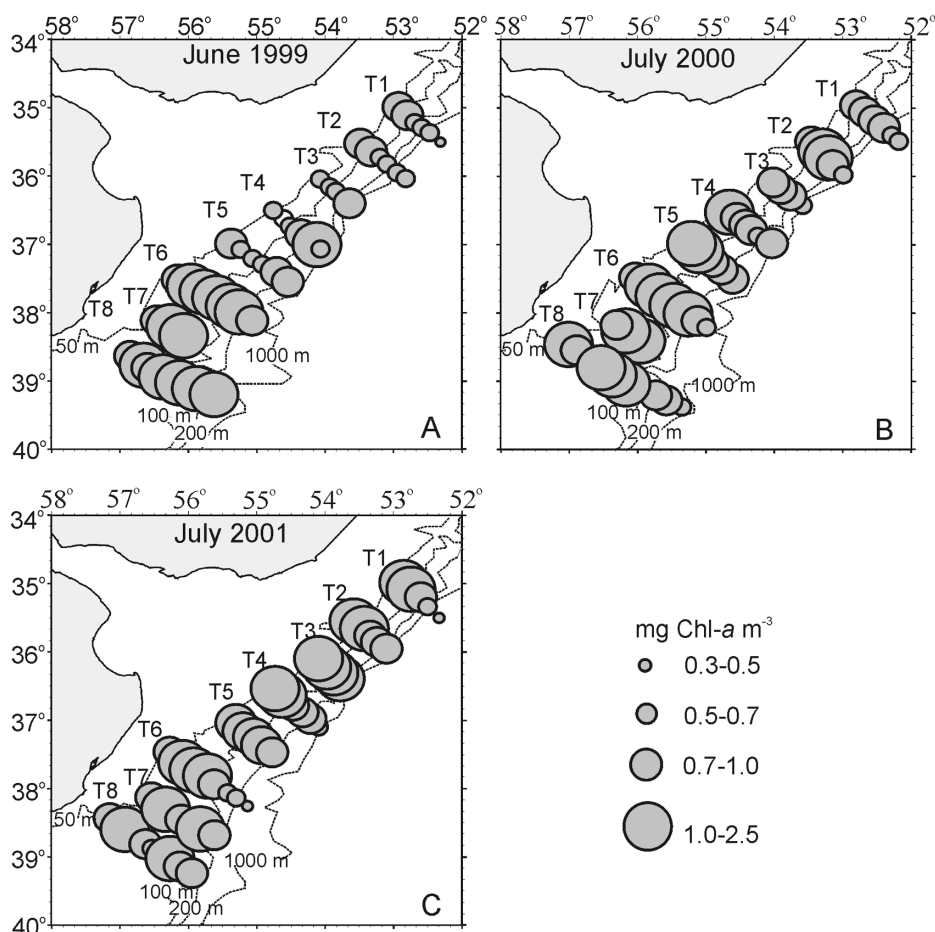
Figure 4. Surface chlorophyll-*a* distribution along transects 1–8 (T1–T8) in (A) June 1999, (B) July 2000, and (C) July 2001 in the sampling area.

waters of T1 (Fig. 3F), indicating the contribution of STSW water. On T5, the temperature varied between 10.5 °C in coastal waters and 7.0 °C below 100 m depth (Fig. 3G), while salinity was relatively homogenous, 33.9–33.8 at 0–150 m depth (Fig. 3H).

In 2001, the coastal and middle shelf waters had surface temperatures of 9.0–12.0 °C, reflecting a smooth gradient in the continental slope front. The presence of warm and salty waters over the offshore sector of T1–T3, with a maximum of 19.6 °C and 35.9 (Fig. 2E,F), indicates the presence of water influenced by STSW. A salinity minimum (29.7) was recorded over the coastal area of T1 from the influence of Rio de la Plata, resulting in another region of maximum gradient. In addition, the temperature and salinity of the deep waters of T1 indicate the contribution of SASW (Fig. 3I,J). On T5, temperature varied between 10.5 and 9.5 °C over the shelf, reaching 8 °C below 100 m depth. However, the salinity was homogeneous (33.65–33.75) over the whole shelf, from 0 to 150 m (Fig. 3K,L).

The surface concentration of Chl-*a* was similar among the 3 yrs and varied between < 0.3 mg m^{-3} in oceanic waters and 2.5 mg m^{-3} in the middle and outer shelf. However, the distribution of Chl-*a* varied among cruises. In June 1999, 52.5% of the

stations had Chl-*a* values between 0.3 and 1.0 mg m^{-3}; in 2000, only 42.0% were in that range, and in 2001, this value diminished to 39.0% (Fig. 4A–C).

SPECIES, DISTRIBUTION, AND ABUNDANCE.—The chaetognaths found along the three winters were: *Eukrohnia hamata* (Möbius, 1875), *Flaccisagitta enflata* (Grassi, 1881), *Flaccisagitta hexaptera* (d'Orbigny, 1836), *Kronitta subtilis* (Grassi, 1881), *Mesosagitta decipiens* (Fowler, 1905), *Mesosagitta minima* (Grassi, 1881), *P. friderici, Pseudosagitta gazellae* (Ritter-Záhony, 1909), *Pseudosagitta lyra* (Krohn, 1851), *Pterosagitta draco* (Costa, 1869), *Serratosagitta serratodentata* (Krohn, 1853), and *S. tasmanica*. Salps were represented by *I. zonaria, I. magalhanica, Ritteriella retracta* (Ritter, 1906), *S. aspera, S. fusiformis,* and *S. thompsoni*. The species present in each year and transect are presented in Table 2. Among the total species captured (18), > 77.0% were found in T1 and T2, while the specific richness decreased toward the south with only 33.3% in T7 and T8.

Salps reached their highest density and frequency in 1999 and decreased in 2000 and 2001 (Fig. 5). In contrast, chaetognaths were frequent (> 84.0% of the stations) in the three winters studied and reached their highest densities in 2000 (Fig. 5). In 1999, transects with greatest abundance of salps were located in the central and northern regions of the study area (T1–T5), reaching 423 ind m^{-3} in one station of T5. The abundance decreased toward the south (T6–T8), with values < 1 ind m^{-3} in T8. In that year, the highest abundance of chaetognaths (> 14 ind m^{-3}) was found in one station of T1, and the lowest abundances were found along T3 and T5 (Fig. 5). In 2000, the abundance of salps was significantly reduced whereas the abundance of chaetognath increased at the outer stations of T1–T3, reaching > 66 ind m^{-3}. In 2001, salps were found only in a few stations in the middle and outer shelf (< 1 ind m^{-3}), while chaetognaths were found in most of the stations, with abundances up to 3.2 ind m^{-3}.

The density of the most abundant species also varied among years and transects (Fig. 6) and even among stations of the same transect. In 1999, the highest mean density occured in T5, where *I. magalhanica* had a mean density of 54.5 ± 90.0 (n = 6) ind m^{-3} and *I. zonaria* a value of 21.8 ± 39.6 (n = 6) ind m^{-3}. However, in one station of the same transect, their abundance reached 301.4 ind m^{-3} for the former and 122.5 ind m^{-3} for the latter. In the case of chaetognaths, the highest mean density was observed in T1, with *P. friderici* being the main contributor with 4.7 ± 4.2 (n = 6) ind m^{-3} (> 14.0 ind m^{-3} in one station in T1). The highest mean density of *S. tasmanica* was in T5 [0.9 ± 0.7 ind m^{-3} (n = 6)] with a maximum density of 2.6 ind m^{-3} recorded in one of the stations (Fig. 6A).

In 2000, the highest mean densities corresponded to chaetognaths and were found in T3 where *S. tasmanica* contributed with 23.4 ± 30.6 (n= 4) ind m^{-3} and *P. friderici* with 7.7 ± 5.0 (n = 4) ind m^{-3}. Along this transect, *S. tasmanica* had a maximum of 66.8 ind m^{-3} in one of the stations and *P. friderici* a maximum of 20.1 ind m^{-3} in another station. The mean density of salps was lower in all transects and *I. zonaria* was the main contributor (Fig. 6B).

In 2001, the mean densities for each transect decreased considerably and the highest mean abundance of *S. tasmanica* [0.7 ± 0.6 ind m^{-3} (n = 4)] was found in T3 and of *P. friderici* [1.6 ± 1.0 m^{-3} (n = 3)] in T7. For salps, the highest mean densities occurred in T1 where 0.2 ± 0.2 (n = 6) ind m^{-3} were recorded for *I. magalhanica* and 0.1 ± 0.01 (n = 6) ind m^{-3} for *I. zonaria*. Maximum density at one transect was 0.6 ind m^{-3} and 0.2 ind m^{-3}, respectively (Fig. 6C).

Table 2. Species found along transects 1–8 (T1–T8) in June 1999 (99), July 2000 (00), and July 2001 (01).

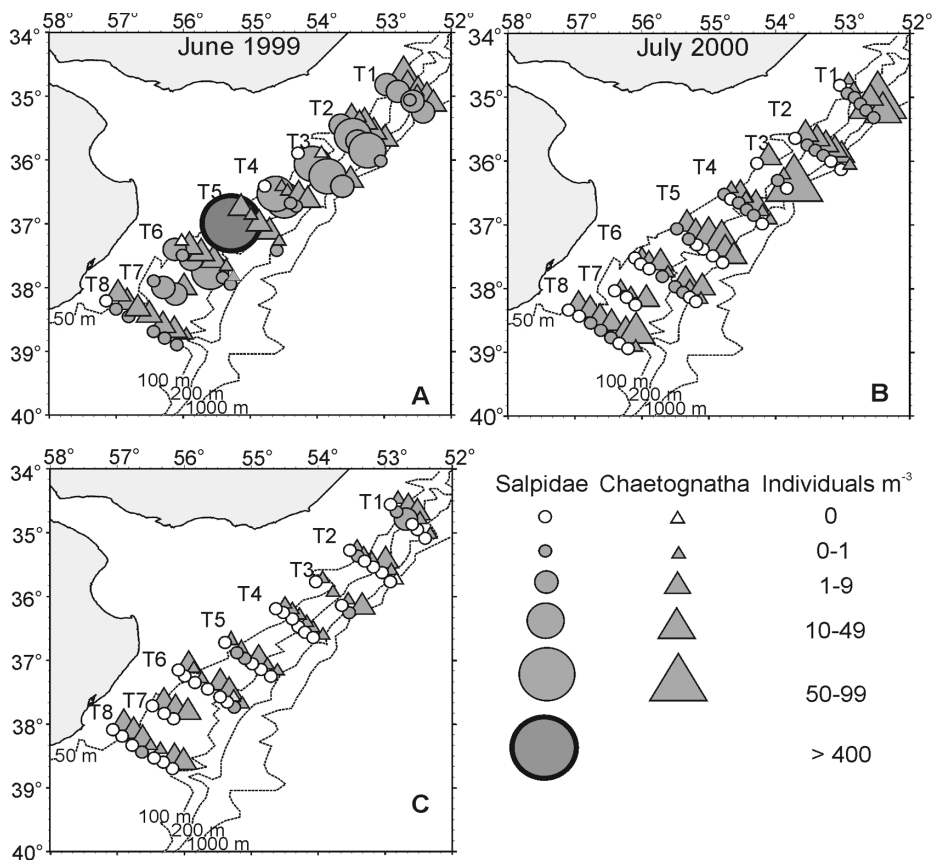|	T 1	T 2	T 3	T 4	T 5	T 6	T 7	T 8
Chaetognatha								
Eukrohnia hamata	99, 00, 01	99	99, 00	99, 00	99	99, 00	–	99, 00
Flaccisagitta enflata	01	99, 01	–	99, 00	–	–	–	–
Flaccisagitta hexaptera	–	99, 01	00	–	–	00	–	–
Krohnitta subtilis	–	–	00	–	–	–	–	–
Mesosagitta decipiens	01	01	–	00	–	–	–	–
Mesosagitta minima	99, 01	00, 01	01	00, 01	–	–	–	–
Parasagitta friderici	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01
Pseudosagitta gazellae	99, 00, 01	99, 00, 01	00	99, 00	00	99, 00	–	00
Pseudosagitta lyra	99, 01	99, 01	99, 01	–	99	99	–	99
Pterosagitta draco	99, 00, 01	01	01	–	–	–	–	–
Serratosagitta serratodentata	99, 01	01	01	–	–	–	–	–
Serratosagitta tasmanica	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01	99, 00, 01
Salpidae								
Iasis zonaria	99, 00	99, 00	99, 00	99, 00	99, 00	99, 00	99, 00	99, 00
Ihlea magalhanica	99	99, 01	99, 00	99, 00, 01	99, 00	99, 00, 01	99, 00, 01	99, 00, 01
Riteriella retracta	01	–	–	–	–	–	–	–
Salpa aspera	99	–	–	–	–	–	–	–
Salpa fusiformis	99	–	–	–	–	–	–	–
Salpa thompsoni	99	99	99	99	99	99	–	–

Figure 5. Total densities of salps and chaetogntahs in stations along transects 1–8 (T1–T8) in (A) June 1999, (B) July 2000, (C) July 2001.

Mean density of copepods varied among years and transects (Fig. 7), with a maximum in 2001 and a minimum in 1999. In 1999, the mean abundance of copepods ranged from 52.0 ± 45.7 (n = 4) to 150.0 ± 27.5 (n= 7) ind m^{-3}. Higher mean abundances were found in the southernmost transects (T6–T8) and the lowest mean abundances in T3–T5. In 89% of the stations, copepods occurred at 15.0–196.0 ind m^{-3}, while in the remaining stations (11%), copepods were absent. In 2000, the top mean abundances occurred in T3 and T8 with values of 196.0 ± 130.9 (n = 4) and 187.0 ± 52.9 (n = 5) ind m^{-3}, respectively. The highest abundances (109.0–377.0 ind m^{-3}) occurred in 53% of the stations, while 9% had no copepods, and the remaining stations varied between 16.0 and 108.0 ind m^{-3}. The highest copepod abundance was measured at one station on T3 (377.0 ind m^{-3}). The highest mean abundance among the three cruises occurred in 2001, and varying between 127.0 ± 91.8 (n = 4) and 328.0 ± 43.4 (n = 4) ind m^{-3} (T3 and T8). Of all stations, 77% had between 140.0 and 398.0 ind m^{-3}, with the highest abundance recorded at one station on T3 (> 398.0 ind m^{-3}). The large error bars in Figure 7 are due to the typically patchy distribution of these planktonic organisms.

The abundance of copepods was positively correlated with both Chl-a (for all 3 yrs) and chaetognath abundance (only in 2000), but was negatively correlated with

the abundance of salps (only in 1999). The abundance of salps showed no correlation with mean salinity or mean temperature; however, salps and the amount of Chl-*a* were negatively correlated (in both 1999 and 2000, Table 3). Salps were more abundant in stations with Chl-*a* values between 0.3 and 1.0 mg m^{-3} (Fig. 8). The total abundance of chaetognaths was positively correlated with temperature, but only in 1999, and this was largely due to the abundance of *P. friderici* (Table 3).
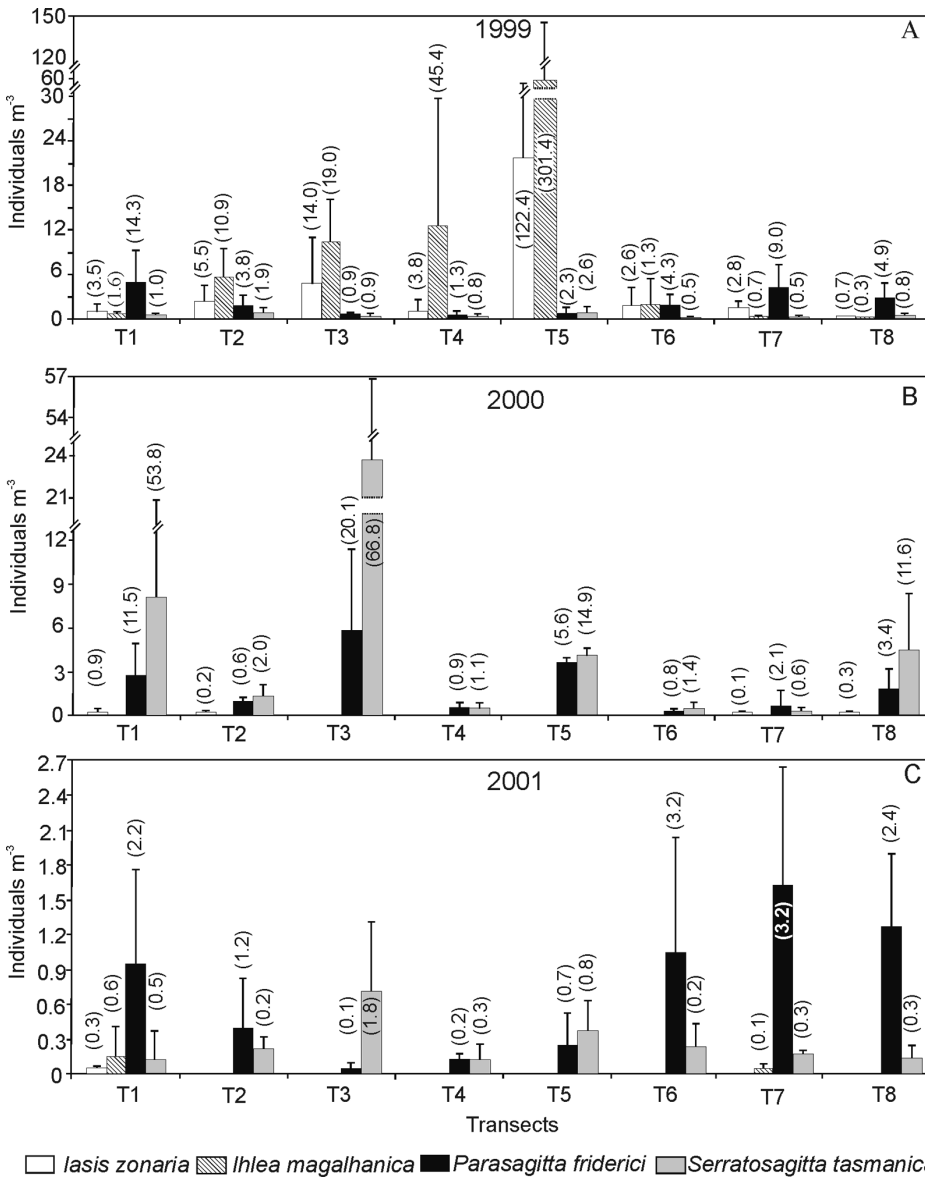

Figure 6. Mean densities of *Ihlea magalhanica*, *Iasis zonaria*, *Parasagitta friderici*, and *Serratosagitta tasmanica* in transects 1–8 (T1–T8) in (A) 1999, (B) 2000, and (C) 2001. The values in parentheses indicate the highest abundance found in a station for each transect (as ind m^{-3}). Note different *y*-axes.

SIZE VS DRY-WEIGHT RELATIONSHIP AND BIOMASS ESTIMATION.—The size of the oozooids of *I. zonaria* varied from 36.0 to 81.0 mm and their blastozooids from 4.0 to 42 mm. The oozooids of *I. magalhanica* varied from 2.0 to 18.0 mm and the blastozooids from 2.3 to 25.0 mm. *Serratosagitta tasmanica* ranged in size from 7.8 to 16.0 mm.

The TL–DW relationship for the oozooids of *I. zonaria* was DW (mg) = $0.0079x^{2.5331}$ (r^2 = 0.98, n = 52) and for the blastozooids DW (mg) = $0.002x^{3.1151}$ (r^2 = 0.96, n = 96). For the oozooids of *I. magalhanica,* it was DW (mg) = $0.0073x^{1.8683}$ (r^2 = 0.96, n = 159) and for the blastozooids, DW (mg) = $0.0345x^{2.5125}$ (r^2 = 0.97, n = 85). This relationship for *S. tasmanica* was DW = $3.8747x^{2.0471}$ (r^2 = 0. 99, n = 100). No evidence was found for rejecting the hypothesis of equality between the slopes for the blastozooids of *I. zonaria* and *I. magalhanica* (P = 0.785). On the other hand, for the oozooids, the slopes of the regression lines differed significantly (P = 0.0033).

The mean values of total biomass (expressed as mg C m^{-3}) for each transect differed among the 3 yrs. In 1999, the highest occurred on T5 (34.9 mg C m^{-3}) and the lowest on T8 (0.8 mg C m^{-3}, Fig. 9A). In 2000, it varied between 1.6 (T3) and 0.1 (T6) mg C m^{-3}, and in 2001, between 0.2 (T7) and 0.01 (T4) mg C m^{-3}. The highest biomass contribution was from salps in 1999 and chaetognaths in 2000 and 2001. Substantial fluctuations were evident among stations along each transect: in 1999, a peak of 180 mg C m^{-3} was found in a station on T5; in 2000, a maximum of 5.74 mg C m^{-3} was measured in a station on T3; and in 2001, only 0.54 mg C m^{-3} was revealed in one station on T1. Salp biomass was significantly higher in 1999 than in 2000 (ANOVA: P = 0.002).

There were no significant differences in the mean biomass of chaetognaths among transects or among years (ANOVA: all Ps > 0.05). Considering the two most abundant species, for *P. friderici*, there were no significant differences in the biomass among transects, among years, or for the transect-year interaction (ANOVA: all Ps > 0.05); for *S. tasmanica*, there was a significant difference in biomass among years
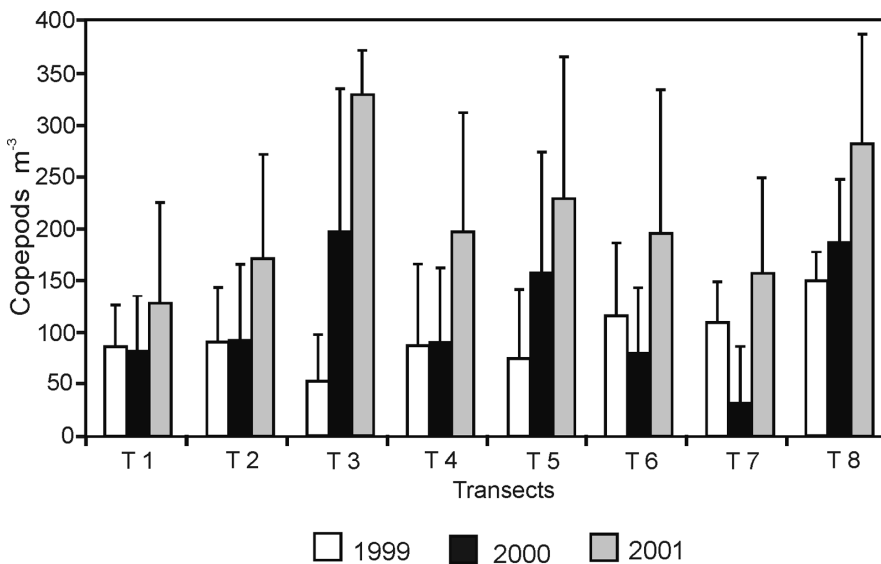

Figure 7. Mean densities of copepods in transects 1–8 (T1–T8) in June 1999, July 2000, and July 2001.

Table 3. Correlations between salps, chaetognaths, copepods, chlorophyll-*a* (Chl-*a*), mean temperature (T°C), and mean salinity (S). Total abundance (T). NS = not significant.

Correlations	1999			2000			2001		
	r	n	P	r	n	P	r	n	P
Salps (T) / Chl-*a*	−0.596	40	< 0.01	−0.410	43	< 0.01	NS	41	
Salps (T) / T°C	NS	43		NS	46		NS	40	
Salps (T) / S	NS	43		NS	46		NS	40	
Salps (T) / copepods	−0.700	40	< 0.01	NS	43		NS	41	
I. zonaria / T°C	NS	43		NS	46			40	
I. zonaria / S	NS	43		NS	46		NS	40	
I. magalhanica / T°C	NS	43		0.304	46	< 0.05	NS	40	
I. magalhanica / S	NS	43		0.294	46	< 0.05	NS	40	
Chaetognaths (T) / T°C	0.350	43	< 0.05	NS	46		NS	40	
Chaetognaths / S	NS	43		NS	46		NS	40	
Chaetognaths (T) / copepods	NS	40		0.517	43	< 0.01	NS	41	
P. friderici / T°C	0.383	43	< 0.01	NS	46		NS	40	
P. friderici / S	NS	43		NS	46		NS	40	
S. tasmanica / T°C	NS	43		NS	46		NS	40	
S. tasmanica / S	NS	43		NS	46		NS	40	
Copepods / Chl-*a*	0.713	40	< 0.01	0.550	43	< 0.01	0.564	41	< 0.01

(ANOVA: P < 0.001), but not among transects or for the transect-year interaction. Tukey comparisons for the biomass of *S. tasmanica* showed that this species' biomass was significantly higher in 2000 than in 1999 and 2001 (ANOVA: P ≤ 0.001).

Discussion

The analysis of salp and chaetognath species found during three winter cruises in the area between 34°S and 39°30′S of the Argentinean Continental Shelf revealed that only four species were always present on the shelf: two salpids (*I. zonaria* and *I. magalhanica*) and two chaetognaths (*P. friderici* and *S. tasmanica*).

The presence of the chaetognaths, *F. hexaptera, P. lyra, P. draco, S. serratodentata,* and the salps, *R. retracta* and *S. fusiformis*, beyond the shelf break (1999 and 2001) coincided with the extension to the south of the warmer and saltier waters of the STSW over the shelf. Despite not being correlated with salinity and temperature, the abundance of *I. zonaria* and *I. magalhanica* reached its highest densities on the STSF (33°S–36°S) in the middle shelf and shelf break. Although both species have a widespread distribution, *I. magalhanica* is considered typically subantarctic (van Soest 1975), while *I. zonaria* is cosmopolitan, having been found mainly in the warm waters of the Atlantic, Indian, and Pacific Oceans (van Soest 1975), and occasionally in the Southern Ocean (Pakhomov and Froneman 1999). Both species were responsible for the large peak in 1999. Although salps are usually found in low densities, they can reach high values at certain times. So far, a few species have been cited as responsible for such peaks: *T. democratica*, *S. fusiformis*, *S. thompsoni,* and occasionally, *I. zonaria*, *Ihlea* spp., and *Cyclosalpa backeri* (Ritter, 1905). High densities of *S. fusiformis* were reported by Bathmann (1988) in the North Atlantic Ocean (> 700 ind m⁻³) and by Huskin et al. (2003) in waters northwest of Spain (225 ind m⁻³). Recently, Licandro
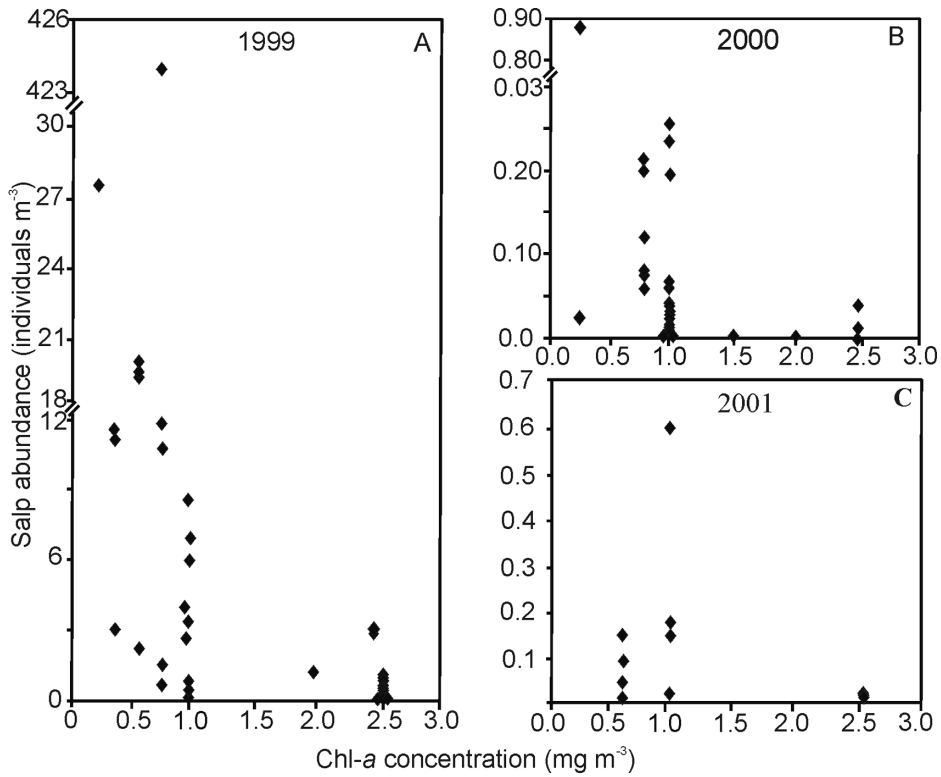
Figure 8. Salp abundance in relation to chlorophyll-*a* concentration in (A) June 1999, (B) July 2000, and (C) July 2001. Negative correlates were significant in 1999 and 2000. Note different *y*-axes.

et al. (2006) reported several outbreaks of *T. democratica* in the Mediterranean Sea with densities of > 23,300 ind 100 m^{-3} (weekly average) in 1990, while *S. fusiformis* reached a mean of 15 ind 100 m^{-3} in 1977.

Previous data on the abundance and frequency of *I. zonaria* and *I. magalhanica* are scarce, but *I. zonaria* has been found close to the Rio de la Plata salinity front (Mianzan and Guerrero 2000, Alvarez-Colombo et al. 2003), reaching a density of 3 ind m^{-3}. It was very frequent (20%–50%) at the Subtropical Convergence Region, south of Africa (Pakhomov et al. 1994), and in Lawson's Bay (Nagabhushanam 1960). In oceanic waters of the western Atlantic Ocean, *I. magalhanica* reached a value of 50 ind m^{-3} (45°00´S, 57°07´W; Daponte et al. 1993), and Yáñez et al. (2009) reported up to 0.3 ind m^{-3} on Juan Fernandez seamounts.

Regarding chaetognaths, the highest densities of *S. tasmanica* and *P. friderici* (the two species not frequently present) were primarily recorded over the frontal zone of the shelf break, but in 2000, when the water temperature along the entire shelf descended ∼2 °C, two species typical of SASW, *S. tasmanica* and *P. gazellae*, were very abundant and widely distributed. The abundance of *P. friderici* diminished from the middle shelf to the shelf break while the abundance of *P. gazellae* increased from the outer shelf to oceanic waters. Mazzoni (1983) found this species mainly in cold waters of the Malvinas Current, outside the shelf break, reaching densities up to 2 ind m^{-3}.
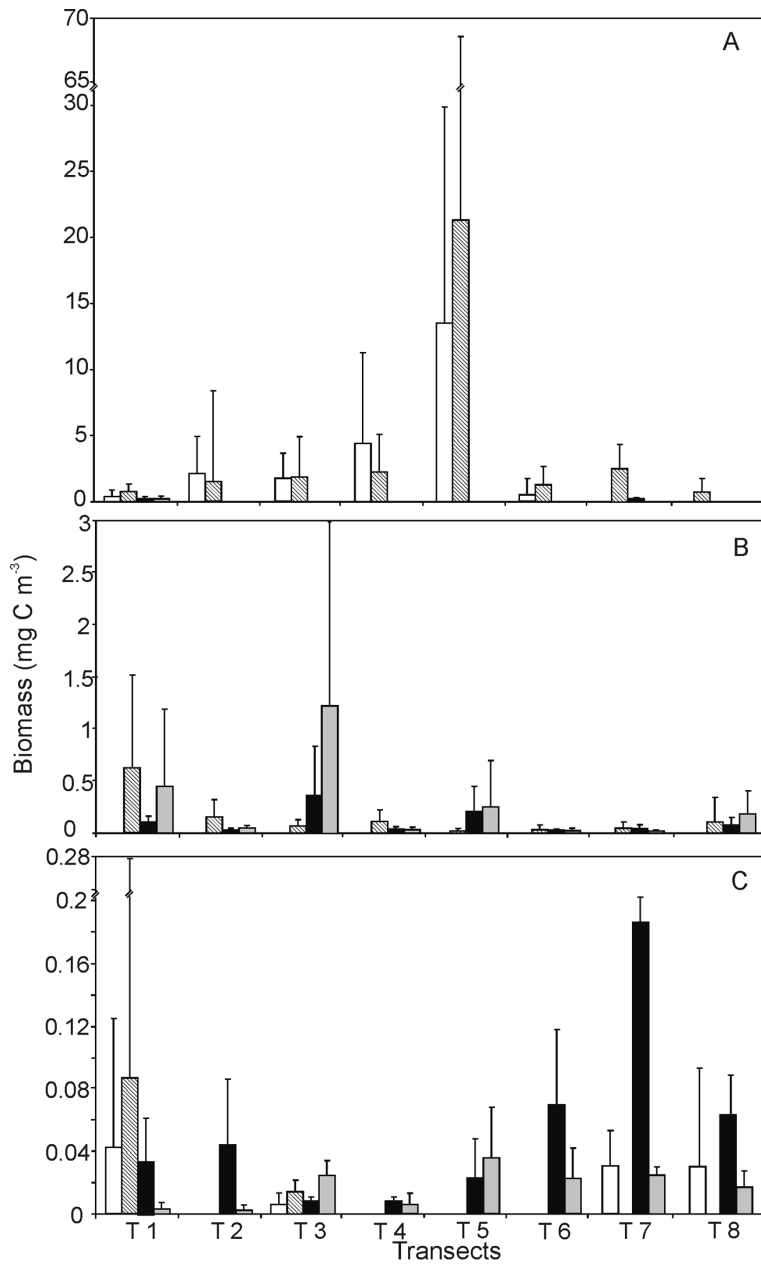
Figure 9. Mean biomass for *Ihlea magalhanica*, *Iasis zonaria*, *Parasagitta friderici*, and *Serratosagitta tasmanica* along transects 1–8 (T1–T8) in (A) 1999, (B) 2000, and (C) 2001. Note different *y*-axes.

The Chl-*a* used in one study were collected remotely. Such data on phytoplankton biomass have been used successfully in the past to analyze temporal and spatial variability of Chl-*a* concentration (García et al. 2004), phytoplankton production (Joint and Groom 2000), and to identify biogeographic regions (González-Silvera et al. 2004). During our study, Chl-*a* ranged from 0.3 mg m^{-3} (oceanic) to 2.5 mg m^{-3} (coastal and middle shelf waters) in accordance with reports from González–Silvera et al. (2004) and Carreto et al. (1995). The amount of chlorophyll and the abundance of salps were negatively correlated as stations with > 4 salps m^{-3} had Chl-*a* values of 0.6–1.0 mg m^{-3}, while higher Chl-*a* concentrations were associated with lower numbers of salps. This correlation agrees with previous observations and is probably related to the fact that high concentrations of phytoplankton can clog the feeding apparatus of salps, which can be fatal. Harbison et al. (1986) showed that *Pegea confederata* (Forsskål, 1775) are unable to feed at high particle concentration and Perissinotto and Pakhomov (1998) found that *S. thompsoni* virtually disappeared when the phytoplankton biomass was > 1.5 mg Chl-*a* m^{-3}.

High abundances of salps may affect the abundance of copepods such as in 1999, when they were negatively correlated. In those stations with > 5 salps m^{-3}, the density of copepods was low (0–198 ind m^{-3}) when compared to the values of 30–2440 copepods m^{-3} reported by Marrari et al. (2004) for the same year and area during early spring, or 0–3406 ind m^{-3} according to Mianzan et al. (2001). Although it is possible that our net mesh size poorly sampled the smaller copepods, this error should have had a similar effect across all of the years sampled. Moreover, the generally low abundance of copepods found in our study is consistent with those reported by Alvarez-Colombo et al. (2003), who found scarce copepods, amphipods, and mysiids at salp densities of 3 ind m^{-3} in the Rio de la Plata area.

The grazing impact of a dense aggregation of salps may affect other planktonic organisms. For instance, *T. democratica* in the northwestern Mediterranean Sea drastically reduced the population of copepods (Licandro et al. 2006). Moreover, *S. fusiformis* in the northern Humboldt Current had a grazing impact of approximately one-half that of the whole crustacean zooplankton community combined (González et al. 2000). Also, Perissinotto and Pakhomov (1998) found that in swarm conditions in the Lazarev Sea, *S. thompsoni* can consume phytoplankton faster than cells can reproduce and possibly may deprive other zooplankton organisms of food sources. For instance, Voronina et al. (2005) showed that high densities of salps may reduce the phytoplanktonic biomass or end the spring bloom (Bathmann 1988), limiting the phytoplankton available for others filter feeding.

The high abundance of chaetognaths in 2000 was correlated to that of copepods. However, this correlation was not apparent in 1999 and 2001, when higher abundances of chaetognaths were found in the frontal regions, STSF, and shelf break, areas where high abundances of copepods have also been recorded in the past (Ramirez and Sabatini 2000, Viñas et al. 2002, Acha et al. 2004). The predation impact of chaetognaths can also have an important influence over copepod populations. For instance, *P. friderici* can remove up to 5.3% of copepod standing stock (Stuart and Verheye 1991), *F. enflata* can consume 7.9% of the daily secondary production in the central equatorial Pacific (Terazaki 1996), and *P. gazellae* can remove 63% of the daily copepod production in the Southern Ocean (Froneman et al. 1998). Consequently, chaetognaths can reduce copepod populations (Øresland 1990) or modify their distributions (Fulton 1984).

The abundance and biomass of salps and chaetognaths in the survey area was related to the physical and biological conditions of the environment. In 1999, the greatest contribution to macrozooplankton biomass was from salps, while in 2000 and 2001, chaetognaths, especially *S. tasmanica* in 2000 and *P. friderici* in 2001, made a greater contribution. When both taxonomic groups co-occurred, the larger sizes of salps resulted in a greater contribution to biomass despite a remarkably lower density. A similar situation was observed between the two salps species where, although the density of *I. magalhanica* was higher than the density of *I. zonaria*, its biomass was lower. The slopes of the DW–TL relationship for the oozooids of the two species were significantly different, possibly reflecting differences in growth, or in size and tunic thickness, among other factors. Oozooids of *I. zonaria* are larger and have a larger stolon, with several blastozooid blocks that are retained in the oozooid before being released (Esnal et al. 1987), contributing to the increase in weight. In *I. magalhanica*, the stolon is smaller and the blastozooids liberated when formed (Daponte and Esnal 1994). Blastozooids of *I. zonaria* are also larger and have wider tunics than those of *I. magalhanica*, but the individuals of both species grow progressively until the moment when the embryos are clearly differentiated. At this point, the increase in weight becomes only slightly greater than in size.

Variation in the quantity of carbon provided by salps and chaetognaths can affect other organisms, principally fishes that feed on chaetognaths (e.g., Cavalieri 1963, Brodeur et al. 2000) and salps (e.g., Kashkina 1986, Clark 1985, Mianzan et al. 2001). The size of the net mesh and the combined impact of salps and chaetognaths could be some of the causes of the low abundance of copepods during the winter of 1999. Lower densities of salps in 2000 and of both salps and chaetognaths in 2001 may have contributed to the higher number of copepods observed in those years. As chaetognaths mainly consume copepods, they can indirectly influence fish population by reducing the availability of food for larvae and adults (Baier and Purcell 1997).

Chaetognaths are common winter inhabitants of the northern shelf while salps tend to be scarce and more patchily distributed. Favorable conditions may develop in winter for *I. zonaria* and *I. magalhanica,* as observed in 1999, when both species bloomed on the shelf. These favorable conditions are probably related to the intrusion of SASW waters after the high temperatures recorded along 1998. Moreover, for the Patagonian region, 1998 was the warmest on record for the last 400 yrs (Jansen et al. 2007), with positive anomalies that exceeded 1.5 °C over almost the entire Argentinian shelf and reaching 2.6 °C in some areas in July (Sanahuja 2007). In 1999, the intrusion of cold water, with a high contribution of nutrients, probably allowed the blooming of *I. zonaria* and *I. magalhanica.* Mianzan and Guerrero (2000) and Alvarez-Colombo et al. (2003) found high abundances of these two species in November 1989 in a station outside the surface salinity front of Rio de la Plata, which is characterized by a high productivity maintained by injection of river nutrients. Similarly, the aperiodic occurrence of dense swarms of *T. democratica* off the coasts of Florida, Georgia, and the Carolinas (USA) was attributed to the intrusion of cool, high nutrient water originating from depths of the Gulf Stream (Deibel and Paffenhöfer 2009).

When blooming, salps dominated in the system in terms of abundance and biomass over copepods and chaetognaths. In addition to their substantial grazing pressure on phyto- and microzooplankton, the rapid increase in the abundance of these species produced a peak of up to 60 times the quantity of C available for other trophic levels such as fishes and birds.

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BMS

Appendix 1. Volume of water filtered at each sampled station in 1999, 2000, and 2001.

1999			2000			2001		
Latitude (S)	Longitude (W)	Volume (m³)	Latitude (S)	Longitude (W)	Volume (m³)	Latitude (S)	Longitude (W)	Volume (m³)
34.9	52.9	27.6	34.9	53.0	137.4	34.9	52.9	39.4
35.1	52.8	57.9	35.0	52.9	124.8	35.0	52.8	57.5
35.1	52.7	174.9	35.1	52.7	109.7	35.1	52.7	139.6
35.2	52.6	62.6	35.2	52.6	85.9	35.2	52.6	159.4
35.3	52.5	77.6	35.3	52.5	65.0	35.3	52.4	31.4
35.4	52.4	73.0	35.4	52.4	25.7	35.5	53.5	40.5
35.6	53.4	34.2	35.6	53.6	156.1	35.6	53.4	39.5
35.6	53.2	89.8	35.6	53.4	179.1	35.7	53.2	119.2
35.7	53.1	101.4	35.7	53.3	210.6	35.8	53.1	45.1
35.9	53.0	105.0	35.8	53.2	228.8	35.9	53.0	67.8
36.0	52.9	110.0	35.9	53.1	256.2	36.0	54.1	49.9
36.0	54.1	39.2	36.1	52.9	320.3	36.1	53.9	55.7
36.0	53.6	56.2	36.0	54.1	339.5	36.2	53.9	38.7
36.2	53.9	79.0	36.1	53.9	365.2	36.3	53.7	65.8
36.4	53.7	43.9	36.2	53.9	385.1	36.4	54.7	44.8
36.5	54.8	37.2	36.3	53.7	18.6	36.5	54.6	71.7
36.6	54.7	30.5	36.5	54.8	288.5	36.6	54.5	78.5
36.7	54.5	47.1	36.6	54.6	303.0	36.7	54.4	48.8
36.8	54.4	55.4	36.7	54.5	303.8	36.8	54.2	78.7
36.9	54.3	35.9	36.8	54.3	303.9	36.9	54.1	55.8
37.0	54.2	61.4	36.8	54.2	315.7	36.9	55.3	56.6
36.9	55.4	11.5	36.9	54.1	338.7	37.0	55.2	57.2
37.0	55.3	13.1	36.9	55.4	27.1	37.1	55.1	32.4
37.1	55.1	28.5	37.0	55.3	43.0	37.2	55.0	35.0
37.3	55.0	48.2	37.2	55.1	68.8	37.3	54.8	43.0
37.4	54.8	50.0	37.3	55.0	93.0	37.4	55.0	120.3
37.5	54.7	59.6	37.4	54.9	116.6	37.4	56.1	45.5
37.5	56.1	14.7	37.4	54.7	146.9	37.5	56.0	77.2
37.5	56.0	21.4	37.4	56.2	301.8	37.5	55.9	61.3
37.6	55.9	32.7	37.5	56.0	285.5	37.7	55.8	58.8
37.4	55.5	39.5	37.7	55.9	259.3	37.8	55.6	48.8
37.8	55.7	47.7	37.6	55.9	160.6	37.8	55.5	46.2
37.5	55.4	70.8	37.6	55.8	243.4	37.9	55.4	11.9
38.0	55.4	91.5	37.7	55.5	219.6	38.1	56.4	37.9
38.1	55.9	50.0	37.8	55.6	201.6	38.2	56.3	48.9
38.0	56.5	75.5	37.9	55.4	182.9	38.3	56.2	21.2
38.2	56.4	69.0	38.1	56.5	319.9	38.4	55.9	31.4
38.3	56.2	40.8	38.2	56.3	348.5	38.3	57.2	34.6
38.4	56.8	74.5	38.3	56.1	369.0	38.4	57.0	51.2
38.7	56.6	77.8	38.5	56.8	122.9	38.7	56.6	52.0
38.8	56.5	39.2	38.6	56.6	106.3	38.8	56.5	38.6
38.9	56.4	87.5	38.7	56.5	85.5	38.9	56.3	25.1
39.0	56.2	110.9	38.8	56.3	68.5	39.0	56.2	41.0
39.1	56.1	68.6	38.9	56.2	48.7			
39.2	55.9	132.4	39.1	56.0	20.1			
			39.2	55.8	381.5			