

Chaetognath spatial distribution and how egg-carrying affects the vertical distribution of *Sagitta tasmanica* off southern Chile

FRANCISCO VILLENAS, SERGIO PALMA and DANIELA SOTO

Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso, Casilla 1020, Valparaíso, Chile.
E-mail: spalma@ucv.cl

SUMMARY: Six chaetognath species were determined, all for the first time, in the inner waters between Reloncaví Fjord and Boca del Guafo, Chile. *Sagitta tasmanica* (85.3%) and *Eukrohnia hamata* (5.8%) were dominant. *Sagitta minima* was collected for the first time in the southern channel and fjord region. The largest chaetognath aggregations were found around the Desertoers Islands, which create a geographic barrier between two microbasins (north and south) with different oceanographic characteristics. *S. decipiens* was distributed mostly in the surface layer (0-50 m), whereas *E. hamata*, *S. chilensis*, *S. minima*, and *S. enflata* were found in deeper waters (50-200 m). The vertical distribution of *S. tasmanica* was homogeneous; mature, egg-carrying individuals were found at greater depths than those without eggs.

Keywords: chaetognaths, spatial distribution, vertical distribution, southern channels, Chile.

RESUMEN: DISTRIBUCIÓN ESPACIAL DE LOS QUETOGNATOS Y CÓMO LA PORTACIÓN DE HUEVOS AFECTA LA DISTRIBUCIÓN VERTICAL DE *SAGITTA TASMANICA* EN EL SUR DE CHILE. – Se determinó la presencia de seis especies de quetognatos, todas ellas registradas por primera vez en aguas interiores comprendidas entre el fiordo Reloncaví y la boca del Guafo, Chile. Las especies dominantes fueron *Sagitta tasmanica* (85,3%) y *Eukrohnia hamata* (5,8%), mientras que *S. minima* se colectó por primera vez en el ecosistema de canales y fiordos australes. Las mayores agregaciones de quetognatos se determinaron alrededor de las islas Desertoers, que constituyen una barrera geográfica entre dos microcuencas de diferentes condiciones oceanográficas. La distribución vertical de *S. decipiens* presentó una preferencia por el estrato superficial, mientras que *E. hamata*, *S. chilensis*, *S. minima* y *S. enflata* se capturaron preferentemente a mayor profundidad. En cambio, *S. tasmanica* se distribuyó homogéneamente en la columna de agua, pero los individuos maduros con huevos se encontraron a mayor profundidad que los que no transportaban huevos.

Palabras clave: quetognatos, distribución espacial, distribución vertical, canales australes, Chile.

INTRODUCTION

Chaetognaths, one of the most important and abundant zooplankton groups in the oceans, typically form dense aggregations in coastal zones (Casanova, 1999). In the oceans, chaetognath abundance follows copepod abundance. Chaetognaths exercise heavy selective predation on copepods; in fact, 10-30% of the copepod biomass is estimated to be

transferred to chaetognaths (Alvariño, 1985; Stuart and Verheye, 1991). Chaetognaths play an important role in pelagic trophic levels. Preyed on mainly by fish, they are intermediaries for the energy flow between the lower and higher trophic levels (Bone *et al.*, 1991). Moreover, as their predatory impact depends not only on their abundance but also on their biodiversity, the chaetognath species composition must be determined in order to understand their real

importance in given geographic areas. Chaetognaths are good water mass indicators (Alvariño, 1965; Bone *et al.*, 1991).

In southern Chile, the channel and fjord ecosystem stretches from Reloncaví Fjord to Cape Horn. Although slightly under 1000 km in length, the area includes some 84000 km of coastline if one includes the contours of the inner islands (Silva and Palma, 2006). This ecosystem is characterised by two-layer estuarine circulation with a surface outflow and deep inflow, different degrees of vertical mixing influenced by the area's geomorphology, variable oceanographic and meteorological conditions, and wide tidal ranges (Silva *et al.*, 1997, 1998).

The oceanographic conditions indicate three water masses in the first 800 m of the oceanic water column off Chiloé Island: Subantarctic Water (SAW), remnants of Equatorial Subsurface Water (ESSW), and Antarctic Intermediate Water (AAIW). The SAW is found at the surface (to around 150 m depth) and it penetrates inward through Boca del Guafo. As the salt water mixes with fresh water from rivers and glaciers, it gives rise to two water masses with estuarine characteristics: Subantarctic Modified Water (SAAMW) and Estuarine Water (EW) (Silva *et al.*, 1998). Between 150 and 200 m depth, remnants of ESSW are found flowing in toward Corcovado Gulf; this, along with the Desertores Islands, creates a bathymetric constriction restricting the passage of ESSW towards Ancud Gulf. The AAIW is below the depth threshold of Boca del Guafo, so this water mass does not penetrate the inner channels (Silva *et al.*, 1998).

Twenty-three chaetognath species have been recorded off the Chilean coast from the genera *Sagitta* (16), *Pterosagitta* (1), *Krohnitta* (2), and *Eukrohnia* (4) (Fagetti, 1995). Only nine of these species have been collected in the inner waters between Boca del Guafo and Cape Horn (Ghirardelli, 1997; Palma and Silva, 2004; Palma, 2006; Villenas and Palma, 2006). However, similar data is lacking for the northern area between Reloncaví Fjord and Boca del Guafo, where Chile's main marine farming centres are found (Silva and Palma, 2006). Consequently, the present study set out to determine the chaetognath species composition and geographic distribution over a broad pelagic area, as well as the relationships between the vertical distribution of *Sagitta tasmanica* and egg-carrying. *S. tasmanica* is the dominant species in Chile's channel and fjord ecosystem (Palma, 2006).

MATERIALS AND METHODS

The CIMAR 10 Fjords Cruise was carried out between 12 and 23 November 2004. Plankton samples were collected at 35 oceanographic stations between Reloncaví Fjord (41°31'S) and Boca del Guafo (43°39'S). The area's oceanographic characteristics indicate two microbasins: one in the north (from Reloncaví Gulf to Ancud Gulf) and one in the south (from Corcovado Gulf to Boca de Guafo). Oblique zooplankton tows were carried out at 28 stations from a maximum depth of 200 m to the surface. In addition, diurnal vertical tows were made from 0 to 50 m and 50 to 200 m depth at seven stations distributed along a north-south transect (Fig. 1). These depths were selected considering the two-layer oceanographic structure of the inner zone (Silva *et al.*, 1997, 1998).

The oceanographic characteristics were described using temperature (°C), salinity and dissolved oxygen concentration (mL L⁻¹) data obtained by CTD casts (Seabird model 25) at 16 stations distributed along a north-south longitudinal section. Bathymetric information was taken from the nautical charts of the Hydrographic and Oceanographic Service of the Chilean Navy (charts 7400, 7410, 7330, 7320, 7300).

Oblique zooplankton tows were performed with Bongo nets (mouth area 0.283 m², mesh size 350 µm) and vertical stratified tows with WP-2 closing nets (mouth area 0.255 m², mesh size 200 µm). Both types of nets were equipped with flowmeters to estimate the volume of water filtered. The zooplankton samples were fixed immediately after collection and preserved in 5% neutral formaldehyde in seawater buffered with borax. In the laboratory, the zooplankton biovolume was estimated using the volume displacement method and the results were expressed in mL of wet plankton per 1000 m³ (mL/1000 m³). Later, all the chaetognath specimens were sorted from the samples, identified to the species level, and counted. Only the dominant species (>5% of the total) were considered for the description of the geographic distribution patterns; abundance was expressed as individuals per 1000 m³ (ind/1000 m³).

Only *S. tasmanica* was considered for the analysis of the relationship between egg-carrying and vertical distribution since this is the predominant chaetognath in the southern ecosystem (Palma, 2006) and the frequency of the remaining species was low. A nonparametric Wilcoxon rank sum test (Wackernagel, 1995) was used to determine differences in the vertical dis-

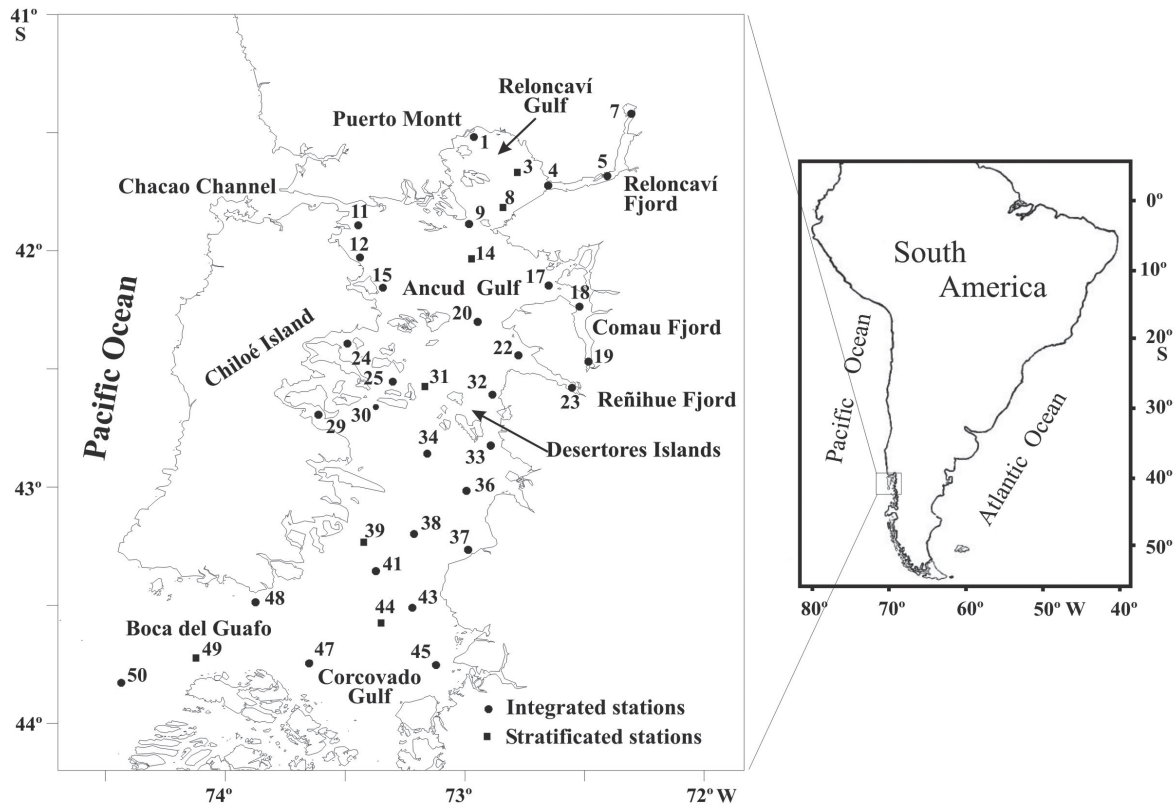


FIG. 1. – Geographic location of sampling stations in the inner waters of southern Chile (CIMAR 10 Fjords Cruise).

tribution given four situations: stratum (abundance at 0-50 vs 50-200 m), fertility (individuals with vs without eggs), stratum/eggs (individuals with eggs at 0-50 vs 50-200 m), and stratum/without eggs (individuals without eggs at 0-50 vs 50-200 m).

Pearson's correlation analysis was used to compare the relative abundance of the species with frequencies over 50% and the weighted averages of the oceanographic variables considered. A logarithmic type transformation was used to make certain that the variables had a multivariate normal distribution (Sokal and Rohlf, 1995).

RESULTS

Oceanographic characteristics

Surface temperatures fluctuated between 11.5 and 13.7°C. They were higher in Reloncaví Gulf and Boca del Guafo and lower in Corcovado Gulf. The northern microbasin was found to have thermal stratification in the first 25 m and a homothermal structure (around 11°C) below 30 m. In Corcovado Gulf, the water column was ho-

mogenous to 50 m depth due to greater vertical mixing caused by the wind; beyond 50 m depth, the temperature dropped to 10°C. Boca del Guafo showed a slight, highly superficial stratification similar to that recorded for the northern microbasin. However, beyond 30 m depth the temperatures fell progressively, reaching 9°C at 200 m (Fig. 2a).

Surface salinity ranged from 11 in Reloncaví Fjord to 32 in Boca del Guafo. In the northern microbasin, a strong vertical gradient was detected in the first 25 m and salinity increased from 32 to 33 at depth. In Corcovado Gulf, the water column was homohaline with an approximate value of 33, whereas towards Boca del Guafo the salinity gradient was greater, increasing from 31 at the surface to 34 at depth (Fig. 2b).

At the surface, dissolved oxygen concentrations were very high (6-8 mL L⁻¹). The northern microbasin was well-oxygenated, exceeding 5 mL L⁻¹ in the first 50 m and dropping to 3 mL L⁻¹ at depth. The 5-mL isoline deepened to 100 m depth between Ancud Gulf and the Desertores Islands. This isoline was more superficial in Corcovado Gulf and reached 50 m in Boca del Guafo. Both microbasins were

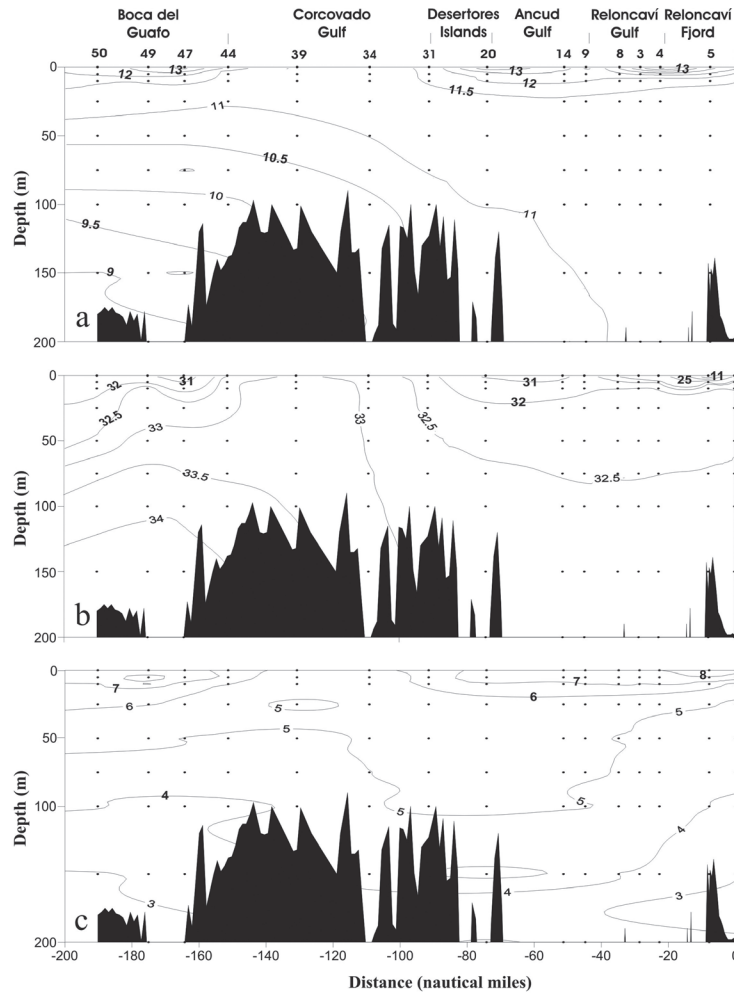


FIG. 2. – Longitudinal section of a) temperature (°C), b) salinity, and c) dissolved oxygen (mL L⁻¹).

well oxygenated in the first 50 m with values that decreased gradually to 3 mL L⁻¹ at depth (Fig. 2c).

Zooplankton biovolume

The zooplankton biovolume was mainly constituted by copepods, chaetognaths, euphausiids and gelatinous organisms (medusae, siphonophores). The biovolume fluctuated between 160 and 2423 mL/1000³, with high spatial variability and an average of 605 mL/1000³. These values were highest in the northern microbasin, particularly in Ancud Gulf. In the southern microbasin, on the other hand, they were low, except at Station 49 in Boca del Guafo (Fig. 3).

Chaetognath species and spatial distribution

Six chaetognath species were identified; all were registered for the first time between Reloncaví Fjord

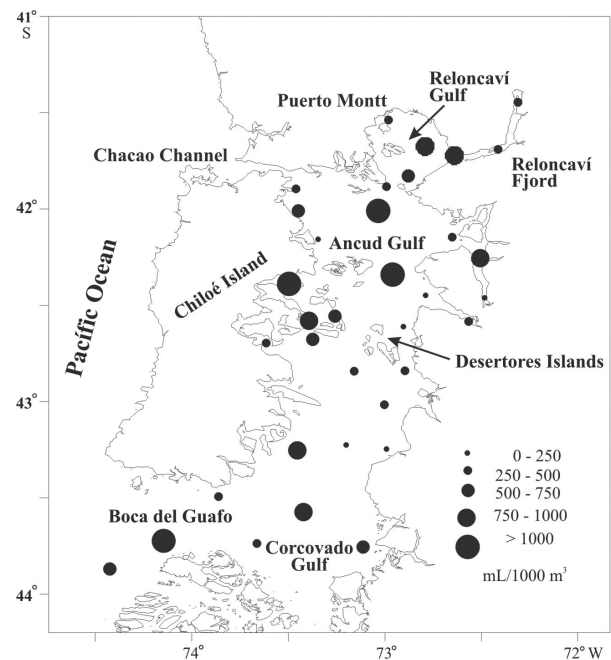


FIG. 3. – Geographic distribution of zooplanktonic biovolume.

and Boca del Guafo. *Sagitta tasmanica* (85.3%) and *Eukrohnia hamata* (5.8%) were the dominant species, followed by the occasional species *Sagitta decipiens* (2.8%), *Sagitta minima* (2.4%), *Sagitta enflata* (2.1%), and *Sagitta chilensis* (1.6%). The most frequent species (>40%) were *S. tasmanica*, *S. minima*, *S. enflata*, and *E. hamata* (Table 1).

The chaetognaths showed a wide geographic distribution and their abundance fluctuated between 243 (Boca del Guafo) and 5866 ind/1000 m³ (De-

TABLE 1. – Average chaetognaths, their dominance frequency, and abundance between Reloncaví Fjord and Boca del Guafo.

Species	Average (ind/1000 m ³)	Dominance (%)	Frequency (%)	Total abundance
<i>Sagitta tasmanica</i>	1598	85.3	97	55925
<i>Eukrohnia hamata</i>	109	5.8	43	3821
<i>Sagitta decipiens</i>	52	2.8	37	1807
<i>Sagitta minima</i>	45	2.4	54	1577
<i>Sagitta enflata</i>	40	2.1	49	1395
<i>Sagitta chilensis</i>	29	1.5	23	1016

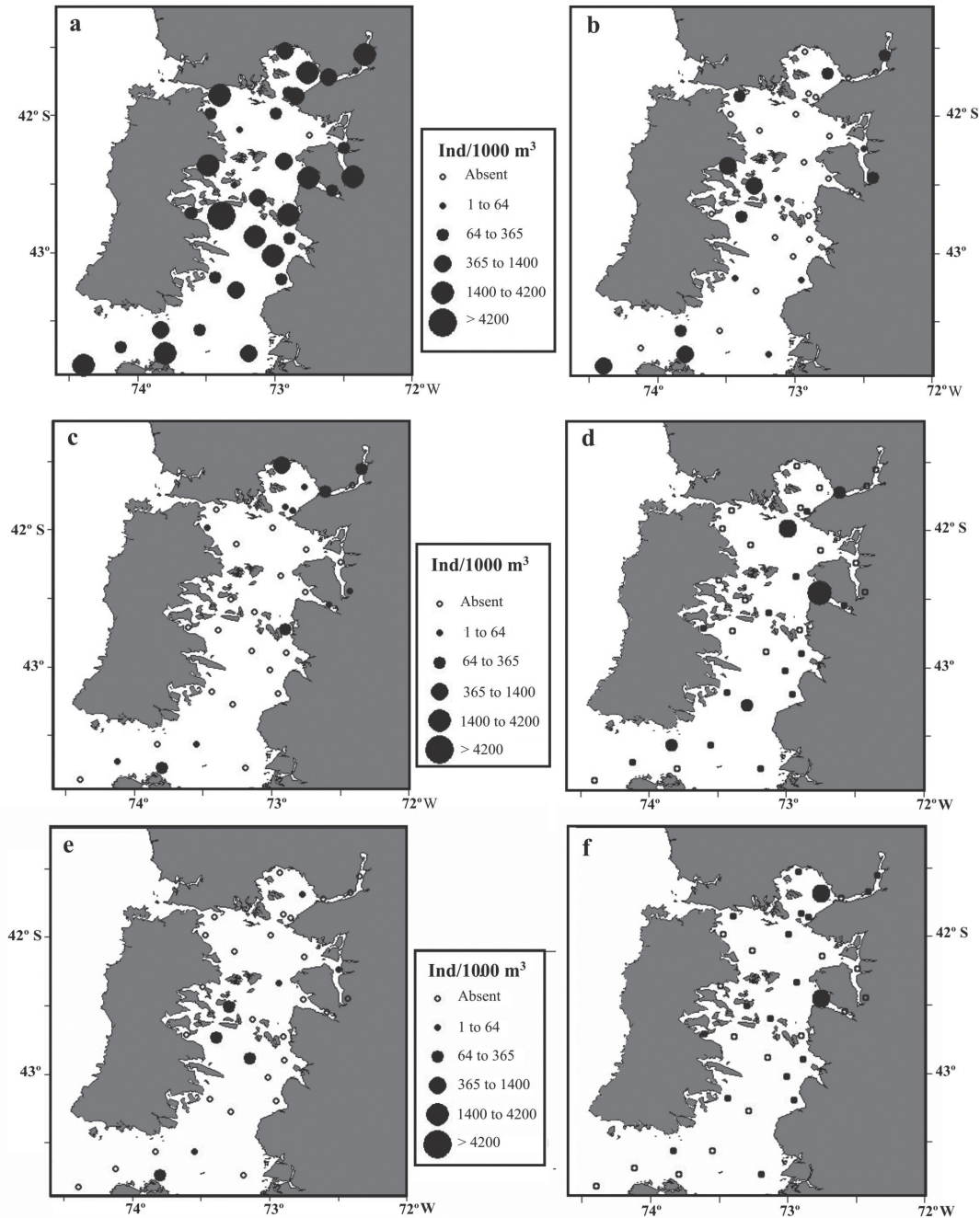


FIG. 4. – Geographic distribution of a) *Sagitta tasmanica*, b) *Eukrohnia hamata*, c) *S. decipiens*, d) *S. enflata*, e) *S. chilensis*, and f) *S. minima*.

TABLE 2. – Pearson's correlation analysis between the relative abundance of the species with a frequency >50% in the study area and the oceanographic parameters. Significant values in bold ($\alpha = 0.05$). STAS: *Sagitta tasmanica*, EHAM: *Eukrohnia hamata*, SMIN: *S. minima*, SENF: *S. enflata*, ZBIO: Zooplanktonic biomass, T: temperature, O₂: dissolved oxygen, and S: salinity.

Variables	STAS	EHAM	SMIN	SENF	ZBIO	T	S	O ₂
STAS	1.00	0.42	0.13	-0.17	-0.25	0.22	-0.22	0.01
EHAM		1.00	0.05	-0.39	0.04	-0.12	0.25	-0.10
SMIN			1.00	0.22	0.03	0.29	-0.27	0.14
SENF				1.00	0.15	-0.21	0.15	0.03
ZBIO					1.00	-0.00	0.08	0.13
T						1.00	-0.86	0.63
S							1.00	-0.38
O ₂								1.00

sertores Islands), averaging 1927 ind/1000 m³. The largest aggregations were located around Desertores Islands, whereas species richness was highest in the northern microbasin.

Sagitta tasmanica was the predominant and most frequent species, averaging 1598 ind/1000 m³ per station. The species was widely distributed throughout the study area, with high-density cores (>5000 ind/1000 m³) around the Desertores Islands (Sta. 22-30). Densities were lower in the southern microbasin (Corcovado Gulf, Boca del Guafo) (Fig. 4a).

Eukrohnia hamata, which averaged 109 ind/1000 m³, was much less frequent (43%) than *S. tasmanica*. *E. hamata* was most dense around the Desertores Islands (>700 ind/1000 m³) and in Boca del Guafo (>400 ind/1000 m³). *E. hamata* was practically absent throughout the sector adjacent to the continental zone with the exception of Comau Fjord (Fig. 4b).

Sagitta decipiens, *S. enflata*, *S. minima*, and *S. chilensis* were occasional species collected at low densities (<200 ind/1000 m³). *S. decipiens* was found in both the northern and southern microbasins, but not around the Desertores Islands. The remaining species were collected mainly in the northern microbasin and around Desertores Islands, but were very scarce in the southern microbasin (Figs. 4c-4f). Only *S. enflata* and *S. minima* had frequencies greater than 49% (Table 1).

Pearson correlation

Pearson's correlation analysis was used to determine a positive linear association between the abundances of *S. tasmanica* and *E. hamata* and between temperature and dissolved oxygen distributions. A negative lineal association was found for *S. enflata* and *E. hamata*, and for temperature and salinity and salinity and dissolved oxygen (Table 2).

TABLE 3. – Vertical abundance (%) of chaetognaths between Reloncaví Fjord and Boca del Guafo.

Species	0-50 m depth (%)	50-200 m depth (%)
<i>Sagitta tasmanica</i>	52	48
<i>Eukrohnia hamata</i>	0	100
<i>Sagitta decipiens</i>	64	36
<i>Sagitta minima</i>	4	96
<i>Sagitta enflata</i>	32	68
<i>Sagitta chilensis</i>	0	100

TABLE 4. – Results of the Wilcoxon ranked-sums test for the abundance of *Sagitta tasmanica*. Situations: Stratum (abundance at 0-50 m vs 50-200 m depth), Fertility (individuals with eggs vs without eggs), Stratum/eggs (individuals with eggs at 0-50 m vs 50-200 m), and Stratum/non eggs (individuals without eggs at 0-50 m vs 50-200 m). Significant values are in bold ($\alpha = 0.05$).

Variables	Z	Wilcoxon	p> Z
Stratum	0.025		0.890
Fertility	2.201		0.028
Stratum/eggs	2.366		0.018
Stratum/non eggs	1.521		0.128

Vertical distribution

Along the north-south transect, *S. decipiens* was found mainly above 50 m depth, whereas most *E. hamata*, *S. enflata*, *S. chilensis*, and *S. minima* were found between 50 and 100 m (Table 3). Only *S. tasmanica* failed to show significant differences in its vertical distribution (stratum: $p > 0.05$) (Table 4), reaching 9°C at 200 m (Fig. 2a).

This species had a more homogenous bathymetric distribution in the northern microbasin (Sta. 3, 8, 14), with slightly higher percentages in the surface layer, whereas in the southern microbasin (Sta. 39, 44, 49) the greatest percentages were observed beyond 50 m depth (Fig. 5).

The vertical distribution of egg-carrying individuals differed significantly from that of non-carrying

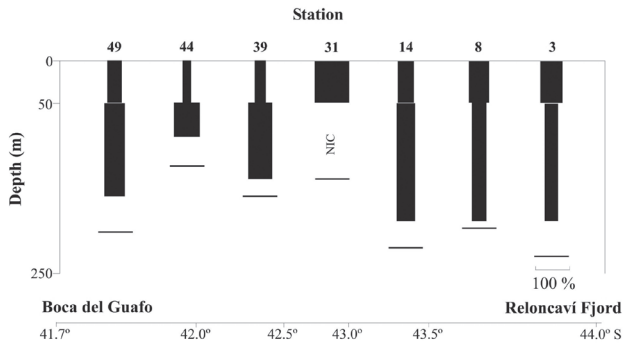


FIG. 5. – Vertical distribution in percentage of *Sagitta tasmanica*. Black bars indicate the depth of the marine floor at the sampling stations. NIC: no individuals were collected.

individuals (fertility: $p < 0.05$, Table 4). Individuals with eggs were found at greater depths (Fig. 6). This distribution pattern was also confirmed by significant vertical distribution values for egg-carrying individuals (stratum/eggs: $p < 0.05$, Table 4).

DISCUSSION

The six species identified constitute new records for the northern sector of Chile's southern inner waters (Reloncaví Fjord-Boca del Guafo), providing complementary information on the geographic distribution of chaetognaths in the southern ecosystem. With the exception of *Sagitta minima*, these species had already been recorded between Boca del Guafo and Cape Horn (Ghirardelli, 1997; Palma *et al.*, 1999; Palma and Aravena, 2001, 2002; Palma and Silva, 2004; Palma, 2006; Villenas and Palma, 2006) (Table 5). Thus, nine species are now cited for the southern channel and fjord ecosystems of Chile and chaetognath abundance is only exceeded by that of the copepods. *S. minima* has been described as a cosmopolitan, warm water oceanic species (Alvariño,

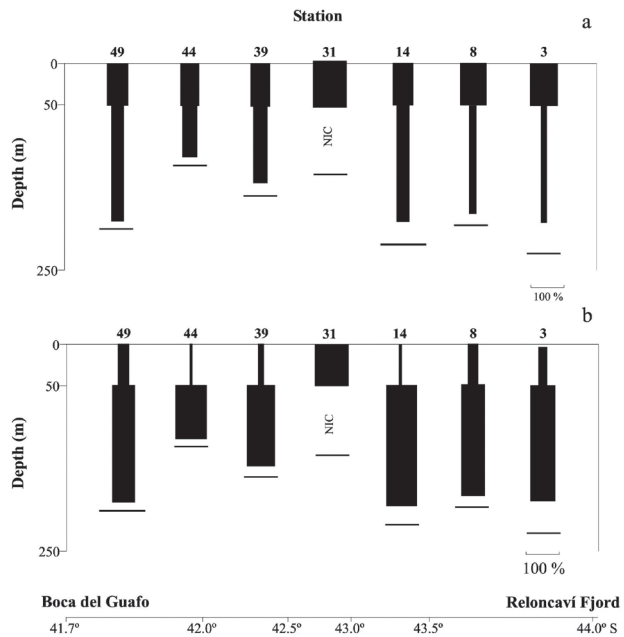


FIG. 6. – Vertical distribution of *Sagitta tasmanica*. a) Individuals without eggs, b) individuals with eggs. Black bars indicate the depth of the marine floor at the sampling stations. NIC: no individuals were collected.

1965) and in the Pacific Ocean it is most common in regions where water masses mix (Bieri, 1959). The colder and less saline inner waters are likely the cause of the scarce abundance of *S. minima* in this region.

The differences in abundance and species richness observed in the chaetognath geographic distribution are responses to the ecosystem, whose complex hydrography is due to the constant exchange of water (external oceanic, inner waters) and the bottom topography (Silva and Palma, 2006). The greatest chaetognath aggregations were recorded around Desertores Islands, coinciding with the area's lower values of zooplankton biovolume. Copepods make

TABLE 5. – Geographic distribution of the chaetognath species recorded off southern Chile. Boca del Guafo (43°40'S), Pulluche Channel (45°47'S), Penas Gulf (47°10'S), Strait of Magellan (52°45'S), and Cape Horn (56°01'S).

Species	Distribution	Source
<i>Sagitta tasmanica</i>	Boca del Guafo to Cape Horn	Ghirardelli, 1997; Palma <i>et al.</i> , 1999; Palma and Aravena, 2001, 2002; Villenas and Palma, 2006
<i>Sagitta decipiens</i>	Boca del Guafo to Cape Horn	Ghirardelli, 1997; Palma and Aravena, 2001, 2002; Villenas and Palma, 2006
<i>Sagitta gazellae</i>	Boca del Guafo to Cape Horn	Ghirardelli, 1997; Palma <i>et al.</i> , 1999; Palma and Aravena, 2001, 2002; Villenas and Palma, 2006
<i>Sagitta enflata</i>	Boca del Guafo to Strait of Magellan	Ghirardelli, 1997; Palma <i>et al.</i> , 1999; Palma and Aravena, 2001, 2002; Villenas and Palma, 2006
<i>Sagitta marri</i>	Penas Gulf to Strait of Magellan	Palma <i>et al.</i> , 1999; Palma and Aravena, 2002
<i>Sagitta maxima</i>	Strait of Magellan	Ghirardelli, 1997; Villenas and Palma, 2006
<i>Sagitta chilensis</i>	Boca del Guafo to Pulluche Channel	Villenas and Palma, 2006
<i>Eukrohnia bathyantartica</i>	Penas Gulf to Strait of Magellan	Palma <i>et al.</i> , 1999; Villenas and Palma, 2006
<i>Eukrohnia hamata</i>	Boca del Guafo to Cape Horn	Ghirardelli, 1997; Palma <i>et al.</i> , 1999; Palma and Aravena, 2001, 2002; Villenas and Palma, 2006

up most of the zooplankton biovolume in the inner waters and such low values suggest that the chaetognaths have a strong trophic impact on the copepods. In the literature, chaetognath voracity and the impact of chaetognath predation over the copepods, their main prey, is widely established (Alvariño, 1965, 1985; Kehayias, 2003; Kehayias *et al.*, 2005; Tönnesson and Tiselius, 2005).

The northern microbasin (Reloncaví and Ancud gulfs) has a more oceanographically stable water column due to less salty estuarine water that favours stratification, high chlorophyll concentrations, and planktonic biomass (Palma and Silva, 2004; Ramírez and Pizarro, 2005), and therefore chaetognath species abundance and richness. On the other hand, the southern microbasin (Corcovado Gulf-Boca del Guafo) is less environmentally stable and is characterised by low biovolume values and zooplankton abundance and diversity due to the constant penetration of SAW and greater mixing caused by the wind and tides (Palma and Silva, 2004; Palma, 2006). The constant input of water favours the presence of mesopelagic species such as *E. hamata* and *S. decipiens*.

Sagitta tasmanica has been found to dominate the chaetognath community in the study area, confirming its wide geographic and bathymetric distribution in the southern channels and fjords (Palma *et al.*, 1999; Palma and Aravena, 2001; Palma and Silva, 2004). Its vertical distribution was much more homogenous in the northern basin (Fig. 5) due to the greater stratification of the salinity in the surface layer. On the other hand, in the southern microbasin, the abundance was greater in the deep layer due to more vertical mixing of the water column in the first 50 m. Moreover, as the circulation pattern in the southern basin indicates a surface (0-30 m) outflow towards the adjacent ocean (Silva *et al.*, 1998), it is likely that the deeper distribution of the specimens in Corcovado Gulf is a strategy used by *S. tasmanica* in order to avoid population advection, as found for *S. friderici* in the coastal waters off South Africa (Gibbons and Stuart, 1994). The Pearson's correlation analysis indicated that the spatial distribution was not related to any of the hydrological conditions studied herein. Thus, the success of *S. tasmanica* in the inner waters is due to its eurythermal and euryhaline nature (Bone *et al.*, 1991). Nonetheless, *S. tasmanica* was positively associated with the spatial distribution of *E. hamata*, although the latter had a much more restricted spatial distribution in the study area. The simultaneous

occurrence of two or more species in a community reflects a certain degree of concordance in the ecological environmental or biological requirements and the species form more or less compact groups according to the similarity of their requirements (Lie *et al.*, 1983; Gasca *et al.*, 1996).

Eukrohnia hamata was the second most abundant species in the area. This species comes from Antarctic and Subantarctic waters (Casanova, 1999) and it moves deeper during its transport to lower latitudes in the eastern South Pacific, where it is found associated with ESSW, which is characterised by lower temperatures and low dissolved oxygen contents (Ulloa *et al.*, 2000). This species enters through Boca del Guafo, avoiding the less salty surface layer (0-50 m), and is distributed below 50 m depth throughout the inner zone, where saltier, colder waters that have low dissolved oxygen contents predominate (Fig. 2) (Silva *et al.*, 1997, 1998). *E. hamata* was always distributed at greater depths, confirming its preference for the deep, cold, and salty conditions of the inner waters south of Corcovado Gulf (Palma and Aravena, 2002). This deeper distribution was also recorded in Scandinavian fjords where *E. hamata* is the predominant chaetognath (Sands, 1980; Oresland, 1985) and in the waters of the eastern Pacific (Bieri, 1959; Ulloa *et al.*, 2000). In spite of these results, *E. hamata* did not present any correlation with the oceanographic parameters recorded. Therefore, its presence in the inner waters is due mostly to the constant advection of the oceanic waters by Chacao Channel in the northern microbasin and Boca del Guafo in the southern microbasin.

Finally, it is interesting to point out the presence of *Sagitta enflata* at some stations. This is the dominant species in the epipelagic waters of the Humboldt Current System, associated with Subantarctic Water (SAW). This species also enters the inner waters ecosystem through Boca del Guafo, where Subantarctic Modified Water (SAAMW; salinity: 31-33) dominates (Silva *et al.*, 1998). Given its lower salinity, this water mass affects the presence of *S. enflata*, which is caught only occasionally (Palma and Silva, 2004). The negative correlation between *S. enflata* and *E. hamata* is due to the fact that *S. enflata* was found throughout the entire water column (0-150 m) in the inner waters, whereas *E. hamata* was found exclusively beyond 50 m depth, where the oceanographic conditions best resemble those of the ESSW (greater salinity, lower temperature, lower dissolved oxygen content).

S. tasmanica did not show any significant differences in its vertical distribution, but the egg-carrying analysis showed that individuals with eggs were collected at deeper depths (Fig. 4). This deeper distribution (50-100 m) results from the ontogenic vertical distribution observed in several chaetognath species such as *S. decipiens* and *S. lyra*, in which adults live deeper where the food is generally less abundant (Kehayias *et al.*, 1994). In general, juveniles live in the upper layers where there is more food available. Furthermore, the distribution of this species at greater depths can be a strategy for remaining in the inner waters, since, according to the circulation pattern described by Silva *et al.* (1998), the less salty surface layer tends to exit through Boca del Guafo towards the adjacent ocean. This retention strategy was also observed for *Sagitta friderici* off the coast of Africa (Gibbons and Stuart, 1994). Other egg-carrying zooplankters have been found to be distributed at greater depths in association with nictimeral migrations that are stimulated by visual contact of predators with their prey (Lampert, 1993; Sekino and Yamamura, 1999).

One of the most important adaptations of the chaetognaths to planktonic life is their transparency; nearly all of their tissues are hyaline except for their sexual glands at maturity. Their transparency is enhanced by rapid digestion and egestion and inconsistent, easily disintegrated feces (Bone *et al.*, 1991; Gasca *et al.*, 1996). Specimens carrying eggs are more vulnerable than those without eggs (semitransparent) because the former are more visible to the predators, particularly under favourable light conditions. Therefore, the specimens with eggs remain at greater depths during the day, decreasing visual contact with predators.

ACKNOWLEDGEMENTS

The authors thank the National Oceanographic Committee for funding the project CONA-C10F 04-11, the captain and crew of the AGOR Vidal Gormaz of the Chilean Navy, and the technicians. Furthermore, we are grateful for the comments made by Professor Nelson Silva, from the Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso. The authors also wish to thank two anonymous referees for their useful comments on the manuscript.

REFERENCES

- Alvariño, A. – 1965. Chaetognaths. *Ann. Rev. Oceanogr. Mar. Biol.*, 3: 115-194.
- Alvariño, A. – 1985. Predation in the plankton realm, mainly with reference to fish larvae. *Invest. Mar. CICIMAR*, 2: 1-122.
- Bieri, R. 1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. *Limnol. Oceanogr.*, 4(1): 1-28.
- Bone, Q., H. Kapp and A.C. Pierrot-Bults. – 1991. *The biology of chaetognaths*. Oxford University Press, New York.
- Casanova, J.P. – 1999. Chaetognatha. In: D. Boltovskoy (ed.), *South Atlantic Zooplankton*, pp. 1353-1374. Backhuys Publishers, Leiden.
- Fagetti, E. – 1995. Chaetognatha. In: J. Simonetti, M. Arroyo, A. Spotorno and E. Lozada (eds.), *Diversidad biológica de Chile*, pp. 174-177. Comisión Nacional de Investigación Científica y Tecnológica, Santiago.
- Gasca, R., J.N. Alvarez-Cadena and E. Suárez-Morales. – 1996. Chaetognath assemblages in the Mexican Caribbean Sea (1991). *Caribb. Mar. Stud.*, 5: 41-50.
- Ghirardelli, E. – 1997. Chaetognaths. In: L. Guglielmo and A. Ianora (eds.), *Atlas of Marine Zooplankton. Straits of Magellan. Amphipods, euphausiids, mysids, ostracods, and chaetognaths*, pp. 241-275. Springer-Verlag, Berlin.
- Gibbons, M.J. and V. Stuart. – 1994. Feeding and vertical migration of the chaetognath *Sagitta friderici* (Ritter-Zahony, 1911) in the southern Benguela during spring 1987, with notes on seasonal variability of feeding ecology. *S. Afr. J. Mar. Sci.*, 14: 361-372.
- Kehayias, G. – 2003. Quantitative aspects of feeding of chaetognaths in the eastern Mediterranean pelagic waters. *J. Mar. Biol. Ass. U.K.*, 83: 559-569.
- Kehayias, G., N. Fragopoulou and J. Lykakis. – 1994. Vertical community structure and ontogenic distribution of chaetognaths in upper pelagic waters of the Eastern Mediterranean. *Mar. Biol.*, 119: 647-6513.
- Kehayias, G., E. Michaloudi and E. Koutrakis. – 2005. Feeding and predation impact of chaetognaths in the north Aegean Sea (Strymonikos and Ierissos Gulfs). *J. Mar. Biol. Ass. U.K.*, 85: 1525-1532.
- Lampert, W. – 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Arch. Hydrobiol. Beih.*, 39: 79-88.
- Lie, U., T. Magnesen, B. Tunberg and D. Aksnes. – 1983. Preliminary studies on the vertical distribution of size-fractions in the zooplankton community in Lindaspollene, western Norway. *Sarsia*, 68: 65-80.
- Oresland, V. – 1985. Temporal size and maturity-stage distribution of *Sagitta elegans* and occurrence of other chaetognath species in Gullmarsfjorden, Sweden. *Sarsia*, 70: 95-101.
- Palma, S. – 2006. Distribución y abundancia de zooplankton en canales y fiordos australes. In: N. Silva and S. Palma (eds.), *Avances en el conocimiento oceanográfico de las aguas interiores chilenas, Puerto Montt a cabo de Hornos*, pp. 107-113. Comité Oceanográfico Nacional-Pontificia Universidad Católica de Valparaíso, Valparaíso.
- Palma, S. and G. Aravena. – 2001. Distribución de sifonóforos, quetognatos y eufáusidos en la región magallánica. *Cienc. Tecnol. Mar.*, 24: 47-59.
- Palma, S. and G. Aravena. – 2002. Distribución estacional y vertical de los quetognatos colectados entre el golfo Corcovado y el estero Elefantes. *Cienc. Tecnol. Mar.*, 25(2): 87-104.
- Palma, S. and N. Silva. – 2004. Distribution of siphonophores, chaetognaths and euphausiids and oceanographic conditions in the fjords and channels of southern Chile. *Deep-Sea Res. II*, 51(6-9): 513-535.
- Palma, S., R. Ulloa and L. Linacre. – 1999. Sifonóforos, quetognatos y eufáusidos de los canales australes entre el Golfo de Penas y Estrecho de Magallanes. *Cienc. Tecnol. Mar.*, 22: 111-142.
- Ramírez, B. and E. Pizarro. – 2005. Distribución de clorofila *a* y feopigmentos en los canales australes chilenos comprendidos entre Puerto Montt y la laguna San Rafael, Chile. *Cienc. Tecnol. Mar.*, 28(1): 45-62.
- Sands, N. – 1980. Ecological studies on the deep-water community of Korsfjorden, western Norway. Populations dynamics of the

- chaetognaths from 1971-1974. *Sarsia*, 65: 1-12.
- Sekino, T. and N. Yamamura. – 1999. Diel vertical migration of zooplankton: optimum migrating schedule based on energy accumulation. *Evol. Ecol.*, 13: 267-282.
- Silva, N., C. Calvete and H. Sievers. – 1997. Características oceanográficas físicas y químicas de canales australes chilenos entre Puerto Montt y Laguna San Rafael (Crucero CIMAR-Fiordo 1). *Cienc. Tecnol. Mar.*, 20: 23-106.
- Silva, N., C. Calvete and H. Sievers. – 1998. Masas de agua y circulación general para algunos canales australes entre Puerto Montt y Laguna San Rafael, Chile (Crucero CIMAR-Fiordo 1). *Cienc. Tecnol. Mar.*, 21: 17-48.
- Silva, N. and S. Palma (eds.). – 2006. *Avances en el conocimiento oceanográfico de las aguas interiores chilenas, Puerto Montt a cabo de Hornos*. Comité Oceanográfico Nacional-Pontificia Universidad Católica de Valparaíso, Valparaíso.
- Sokal, R. and F.J. Rohlf. – 1995. *Biometry: The principles and practice of statistics in biological research*, 832 pp. W.H. Freeman and Company, New York.
- Stuart, V. and H.M. Verheye. – 1991. Diel migration and feeding patterns of the chaetognaths, *Sagitta friderici*, off the west coast of South Africa. *J. Mar. Res.*, 49: 493-515.
- Tønnesson, K. and P. Tiselius. – 2005. Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. *Mar. Ecol. Prog. Ser.*, 289: 177-190.
- Ulloa, R., S. Palma and N. Silva. – 2000. Bathymetric distribution of chaetognaths and their association with water masses off the coast of Valparaíso, Chile. *Deep-Sea Res.*, 47(11): 2009-2027.
- Villenas, F. and S. Palma. – 2006. *Sagitta chilensis* nueva especie de chaetognato en fiordos australes chilenos (Chaetognatha, Aphragmophora, Sagittidae). *Invest. Mar., Valparaíso*, 34(1): 101-108.
- Wackernagel, H. – 1995. *Multivariate geostatistic, an introduction with applications*. Springer-Verlag, Berlin.

Scient. ed.: R. Anadón.

Received September 3, 2007. Accepted June 27, 2008.

Published online November 25, 2008.