

Epipelagic siphonophore assemblages associated with water masses along a transect between Chile and Easter Island (eastern South Pacific Ocean)

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We analyze for the first time the spatial distribution of siphonophores in relation to water masses along a 3750-km oceanic transect between the Chilean coast and the Easter Island (27° S), a sector scarcely known of eastern South Pacific Ocean. Thirty-one siphonophore species were identified; Sulculeolaria turgida and Vogtia glabra were recorded for the first time in this sector. The most abundant species were Muggiaea atlantica (29.2%), Eudoxoides spiralis (24.5%) and Lensia subtilis (13.1%). Two different siphonophore assemblages east and west of 76° W, associated respectively with Subantarctic Water and Subtropical Water masses, can be used as water mass indicators. The former included the three most abundant species, whereas the latter showed greater species richness. This study provides basic knowledge on spatial distribution of siphonophores, which is important to develop future research focused on understanding the ecological role and biological processes driven by planktonic organisms in the southeastern Pacific Ocean.

INTRODUCTION

The eastern South Pacific (ESP) region is characterized by the Humboldt Current System (HCS) off the western coast of South America. Off northern Chile, the extreme eastern boundary of this system between 0 and 100 m depth consists of Subantarctic Water (SAAW), with relatively low temperatures and salinity. The western portion of the HCS is formed of Subtropical Water (STW) near the surface, with relatively high temperatures and salinities, as well as low nutrient concentrations typical of the anticyclonic South Pacific gyre, which reaches 300 m in depth. Equatorial Subsurface Water (ESSW) was found between 100 and 400 m depth and was characterized by high salinity and an oxygen minimum zone (OMZ). Low salinity Antarctic Intermediate Water (AAIW) was found between 400 and 1000 m depth (Reid, 1973; Silva, 1992; Strub *et al.*, 1998; Moraga *et al.*, 1999).

The coastal zone of the ESP is characterized by high biological productivity, capable of sustaining the high fishery activity typical of the HCS (Alheit and Bernal, 1993). In contrast, some of the most oligotrophic areas occur in the western portion of the study area within the STWs of the South Pacific anticyclonic gyre (Vinogradov, 1991). Both coastal and oceanic waters host diverse populations of gelatinous carnivores (medusae, siphonophores, ctenophores and mollusks) that compete with other species for common trophic resources (Purcell, 1997; Pagès *et al.*, 2001).

Most studies on gelatinous zooplankton in the ESP have been carried out within the coastal waters of the HCS. Strong seasonal fluctuations in abundance have been recorded in this zone; population levels peak in spring and summer when mono- or bi-specific genera of medusae, siphonophores and/or ctenophores form

dense aggregations (Palma and Rosales, 1995; Pagès *et al.*, 2001; Palma and Apablaza, 2004). Conversely, information on gelatinous zooplankton in the STWs of the ESP is scarce and mainly restricted to the distribution and abundance patterns of 15 calycophore siphonophore species found near the surface (0–10) around Easter Island (Palma, 1999). Although they seemed to provide early evidence of a link between siphonophore distribution and different water masses, these findings were inconclusive because of the lack of a data set from a coast-to-offshore transect (Alvariño, 1971).

The analysis of oceanic transects has notably advanced the zoogeography of marine plankton in the Pacific and the understanding of the macroscale distribution of chaetognaths and euphausiids (Bieri, 1959; Brinton, 1962). The evidence gathered from these studies suggests that the distribution of planktonic species is closely related to the oceanographic properties of distinct water masses where they occur. Conversely, a comprehensive study (see Alvariño, 1971) on geographic and vertical siphonophore distribution patterns in the Pacific Ocean suggested that most species are cosmopolitan and related to the distribution of the 200-m depth isotherms. Because neither the water-mass-based nor the Alvariño's hypotheses had not yet been tested on siphonophores in the ESP, this study set out to test the link between the distribution and abundance patterns of siphonophores as related to the water mass structure in the ESP. For this purpose, we used a comprehensive sampling procedure in epipelagic waters (0–200 m) across a 3750-km ocean transect between continental Chile and Easter Island.

METHOD

Sampling and laboratory procedures

Zooplankton samples were obtained at 32 oceanographic stations during the Cimar 5 Oceanic Islands Cruise carried out between 15 and 28 October 1999 over a 3750-km oceanic transect between Caldera (27°00' S, 70°52' W) and Easter Island, Chile (27°10' S, 109°20' W) (Fig. 1).

Oceanographic data including temperature, salinity and dissolved oxygen were obtained from the Cruise Data Report (Rojas *et al.*, 2005). Water masses were diagnosed on the basis of T-S diagrams, and their percentage of participation in the water mixture was determined using the triangle mixing method (Mamayev, 1975) and the T-S water types defined by Ulloa *et al.* (Ulloa *et al.*, 2000). A water mass was considered to be predominant in a mixture when its participation was $\geq 50\%$. Surfer 7 software package (Golden Software) was used to draw the oceanographic figures.

Zooplankton samples were collected day and night at 32 stations using oblique tows from a maximum depth of 200 m to the surface. Tows were made using Bongo nets with 200- μm mesh size and a 60-cm diameter mouth. The nets were towed at a mean speed of 20 m min^{-1} and were equipped with a flowmeter to determine the volume of water filtered. Samples were preserved in 5% borate-buffered seawater formalin.

Based on the polymorphic structure of the siphonophores, larval and adult colonies were counted for the Physonectae; for the Calycophorae, polygastrics (nectophores) and eudoxids (bracts and gonophores) were counted. All species were identified based on the current status of taxonomic information (Pugh, 1999). The relative abundance by species was standardized as the number of individuals 1000 m^{-3} (individuals 1000 m^{-3}).

The species richness for each station was calculated, and a cluster analysis was carried out, using the $\log(x + 1)$ relative abundance transformation to describe the species distribution patterns and to determine the sample group with the greatest specific affinity. The Bray-Curtis Index of Similarity (Bloom, 1981) was used to perform the clusters analysis.

RESULTS

Oceanographic characteristics

Temperature and salinity at the sea surface increased progressively across the transect from the coastal zone (13°C, 34.4) to Easter Island (21°C, 36.1). The vertical distribution of temperature and salinity showed a coastal mixed layer $\sim 40\text{-m}$ thick that deepened to $\sim 150\text{ m}$ near the island. The thermocline and the halocline, with vertical gradients of ~ 0.04 and $0.006^\circ\text{C m}^{-1}$, also deepened towards the west; their cores were located around 50 and 250 m depth near Easter Island (Fig. 2).

Off the coastal zone, the vertical salinity distribution showed a shallow minimum (<34.4), centered on 100 m. Toward the west (91° W), this salinity minimum deepened to $\sim 250\text{--}300\text{ m}$ (Fig. 2). Below the shallow salinity minimum, salinity increased to form a relative salinity maximum (>34.5) centered around 200 m at the coast and below 300 m at 95°W. A well-oxygenated surface layer was found along the entire transect ($>5 \text{ mL O}_2 \text{ L}^{-1}$). This layer was almost homogeneous, being shallower in the coastal zone (40 m) and deeper near Easter Island (250 m) (Fig. 2). Dissolved oxygen decreased rapidly below this layer to form an oxygen minimum ($<3 \text{ mL O}_2 \text{ L}^{-1}$) centered on 200 m in the coastal zone where it formed an OMZ ($<1 \text{ mL O}_2 \text{ L}^{-1}$).

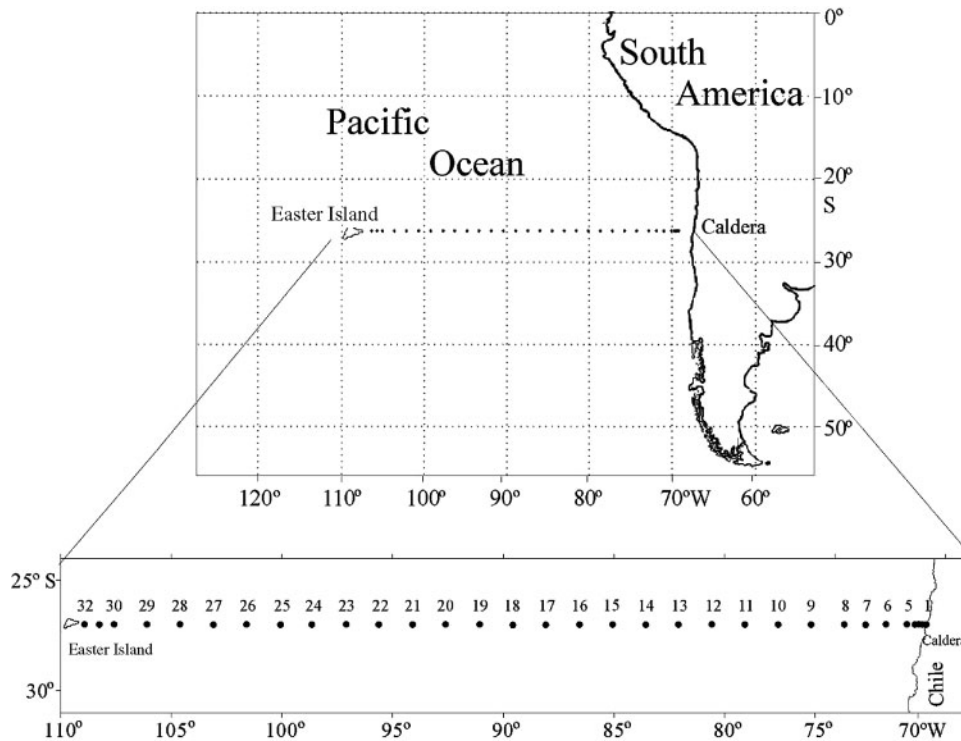


Fig. 1. Geographic location of the sampling stations in the oceanic transect between Caldera and Easter Island, Chile.

Water masses

STW was detected from 500 km off the coast to Easter Island, with 50–90% participation in the water mix and increased thickness toward the west, from 100 m at 77° W to 300 m at 110° W. STW was characterized by temperatures of 16–21°C, salinities of 34.7–36.2 and dissolved oxygen $>5 \text{ mL L}^{-1}$. The vertical structure of temperature, salinity and dissolved oxygen in the STW was homogeneous, and the mixed layer increased from 50 m on its eastern boundary to up to 150 m near Easter Island (Fig. 3).

SAAW was observed at the surface layer of the coastal zone, extending 2000 km to the west below the STW as a thin layer ~ 100 m thick, centered on 250 m depth. SAAW was detected as a continuous core occupying 50–70% of the mixture from Station 2 to Station 5 and as a sequence of discontinuous 50% cores between Station 5 and Station 18. In the transect, this water mass was typified by temperatures between 11 and 16°C, salinities between 34.2 and 34.5 and dissolved oxygen between 3 and 5 $\text{mL O}_2 \text{ L}^{-1}$ (Fig. 3).

ESSW showed participation percentages ranging from 50 to 80%, centered around 250 m near the coast and deepening to the west. ESSW was typified by temperatures of 8–12°C, salinities of 34.4–34.7 and dissolved oxygen of

$<3 \text{ mL O}_2 \text{ L}^{-1}$; near the continental slope, dissolved oxygen declined to $0.5 \text{ mL O}_2 \text{ L}^{-1}$ in the OMZ (Fig. 3).

Species composition and richness

The taxonomic analysis of the polygastric and eudoxid phases determined 31 species of siphonophores, belonging to the suborders Physonectae (1 species, *Agalma elegans*) and Calycophorae (30 species) (Table I). *Sulculeolaria turgida* and *Vogtia glabra* were recorded for the first time in this area of the Pacific Ocean. The most abundant species were *Muggiaea atlantica* (29.2%), followed by *Eudoxoides spiralis* (24.5%), *Lensia subtilis* (13.1%), *A. elegans* (7.1%), and *Abylopsis tetragona* (6.0%); together these species constituted 80% of the total siphonophores (Table I). Species richness ranged from 5 to 18 species, with the lowest values found near coastal stations and at stations 12, 21 and 22. There was a gradual increase in species richness towards Easter Island, where the number of species ranged between 10 and 18.

Similarity analysis

Based on the Bray-Curtis similarity analysis, two groups were yielded (Fig. 4).

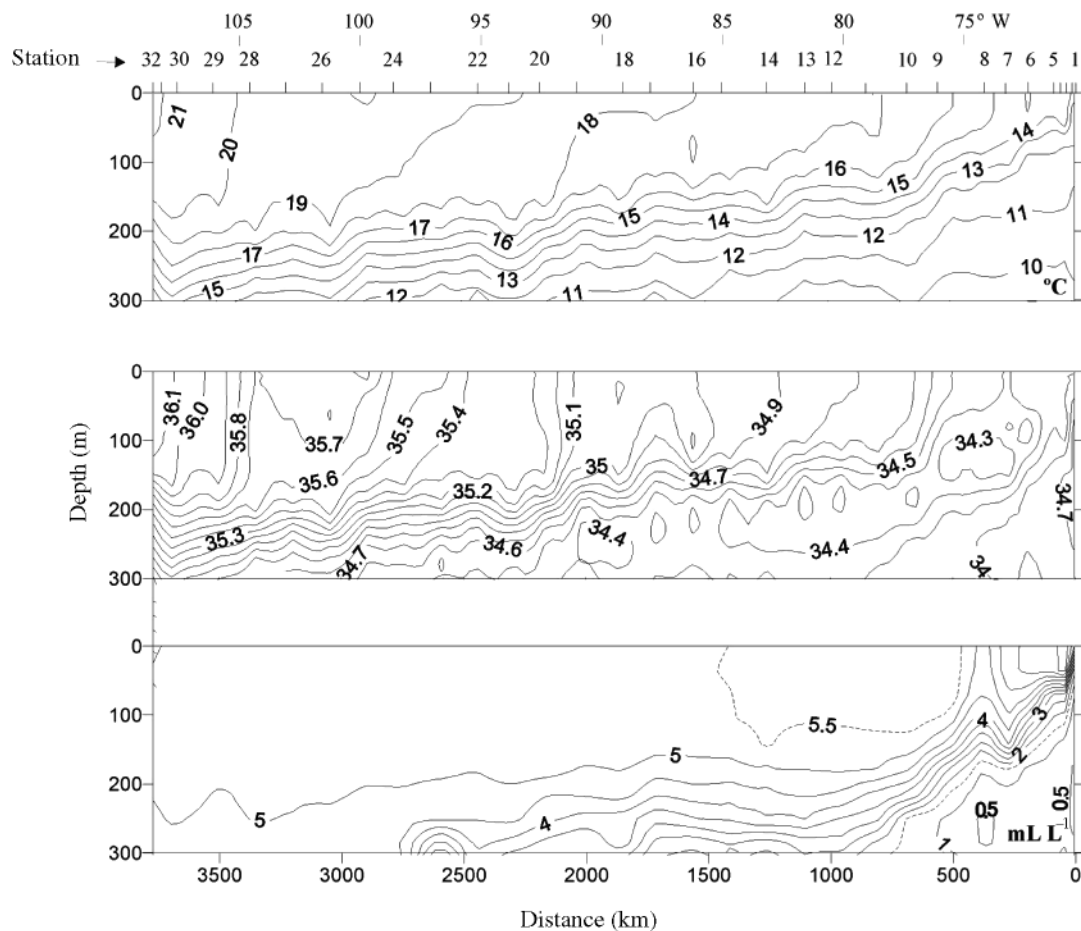


Fig. 2. Vertical distribution of temperature, salinity and dissolved oxygen in an oceanic transect.

Group A

These continental stations (Stations 1–9; 71–76° W) were typified by abundant *M. atlantica*, *A. elegans* (larval and adult colonies) and *A. tetragona* (Fig. 3), along with some less abundant species including *Lensia multicristata* and *Rosacea plicata*. The extremely abundant *M. atlantica* was only collected at the easternmost 10 stations, with a maximum at Station 8. Eudoxids were scarce, with a maximum at the same station. Adult colonies of *A. elegans* were less numerous than larval colonies and occurred in the more western stations, reaching 90° W. *Abylopsis tetragona* was distributed across the length of the oceanic transect, even at Easter Island. Most nectophores were collected near the continental coast (Stations 1–8), with a maximum at Station 8. The eudoxid distribution pattern was similar to that of the nectophores, with a maximum at the same station.

Group B

This group encompassed species widely distributed throughout the oceanic stations (i.e. *Abylopsis eschscholtzi*,

Bassia bassensis, *Diphyes bojani*, *E. spiralis*, *Lensia campanella* and *L. subtilis*) and less abundant or rare species (i.e. *Abyla trigona*, *Amphicaryon acaule*, *Chelophyes appendiculata*, *Chelophyes contorta*, *Eudoxoides mitra*, *Hippopodius hippopus*, *Lensia cossack*, *Lensia hardy*, *Sphaeronectes irregularis*, *Sulculeolaria chumi* and *Sulculeolaria monoica*). Group B also encompassed two sub-groups: the first included *E. spiralis*, *D. bojani* and *B. bassensis*, the most abundant species in the central zone of the oceanic transect (Fig. 3). *Eudoxoides spiralis*, the most abundant, was primarily found between 76 and 96° W with concentrations surpassing 200 individuals 1000 m⁻³ at most stations; eudoxids were scarce but showed the same distribution pattern across the oceanic transect. For *D. bojani*, the number of eudoxids was higher than that of nectophores at various stations, particularly in the central zone (85–91° W). *Bassia bassensis* was found at low densities across the entire transect (<50 individuals 1000 m⁻³). The second group (i.e. *L. campanella*, *L. subtilis* and *A. eschscholtzi*) showed mainly oceanic distributions (west of 90° W) with isolated abundance cores (Fig. 3). *Lensia subtilis* was the most abundant, with two high abundance cores at

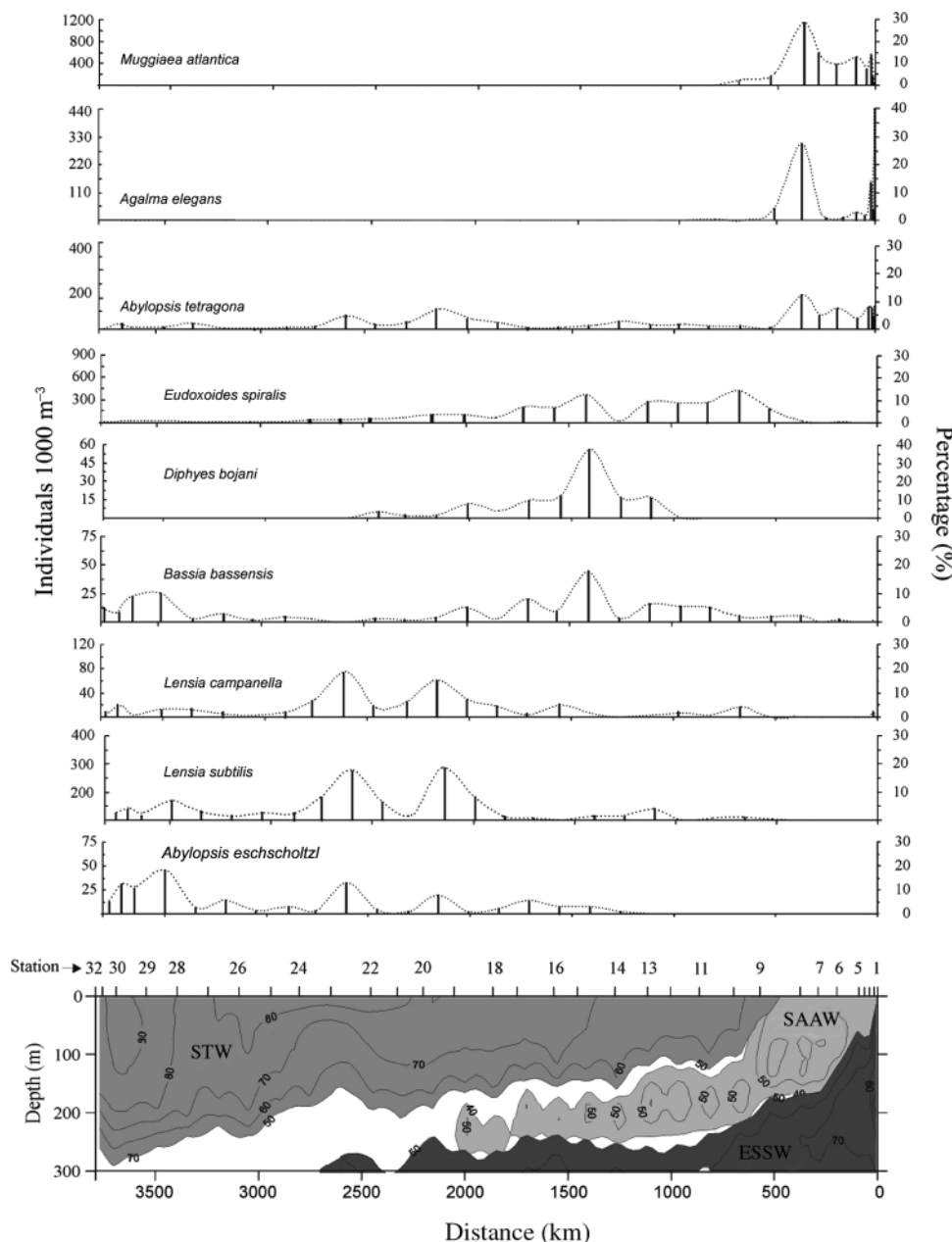


Fig. 3. Distribution of siphonophore species associated to water masses in the oceanic transect. SAAW, Subantarctic Water; STW, Subtropical Water; ESSW, Equatorial Subsurface Water.

90–99° W and 104–108° W. Eudoxids of the three species were scarce, except for *A. eschscholtzi* at the stations near Easter Island.

DISCUSSION

A distinctive pattern of oceanographic conditions was apparent in this study, STW was predominant from 78° W to the end of westernmost stations; conversely, SAAW predominated in the coastal zone. STW is

characteristic of central ocean gyres and has lower nutrient concentrations than SAAW (Reid, 1973). Consequently, coastal waters are expected to have higher productivity than the oligotrophic STW. In addition, the enhanced productivity of coastal water is strengthened by the presence of ESSW, which is characterized by nutrient concentration maxima associated with the OMZ (Reid, 1973). These high nutrient, low dissolved oxygen values are characteristic of the ESP and represent water originating off Peru and transported southward by the

Table I: Siphonophores collected between Caldera and Easter Island, ranked by order of abundance

Species		Total (individuals 1000 m ⁻³)	Percentage (%)	SAAW		STW		All Transect	
				Abundance ln (x + 1)	Geometric mean	Abundance ln (x + 1)	Geometric mean	Abundance ln (x + 1)	Geometric mean
<i>Muggiaea atlantica</i>	ne	4016	29.23	8.30	184				
	eu	189							
<i>Eudoxoides spiralis</i>	ne	3365	24.49					8.12	58
	eu	316							
<i>Lensia subtilis</i>	ne	1798	13.09			7.50	29		
	eu	9							
<i>Agalma elegans</i>	la	973	7.08	6.88	34				
	co	1012							
<i>Abylopsis tetragona</i>	ne	826	6.01					6.72	25
	eu	2715							
<i>Lensia campanella</i>	ne	430	3.13			6.07	11		
<i>Bassia bassensis</i>	ne	415	3.02					6.03	10
	eu	230							
<i>Abylopsis eschscholtzi</i>	ne	287	2.09			5.66	9		
	eu	16							
<i>Diphyes bojani</i>	ne	286	2.08			5.66	12		
	eu	428							
<i>Lensia hardy</i>	ne	204	1.48						
<i>Chelophyes appendiculata</i>	ne	167	1.22					5.12	6
	eu	6							
<i>Eudoxoides mitra</i>	ne	142	1.03			4.96	6		
	eu	110							
<i>Lensia hotspur</i>	ne	133	0.97					4.90	9
<i>Chelophyes contorta</i>	ne	133	0.96			4.89	17		
	eu	7							
<i>Lensia fowleri</i>	ne	106	0.77					5	7
	eu	3							
<i>Sulculeolaria chuni</i>	ne	104	0.76			4.66	7		
<i>Sphaeronectes irregularis</i>	ne	89	0.65			4.50	4		
<i>Hippopodius hippopus</i>	ne	84	0.61			4.45	9		
	eu	15							
<i>Lensia cossack</i>	ne	60	0.43					4.67	6
<i>Abyla trigona</i>	ne	22	0.16			3.12	2		
<i>Lensia multicristata</i>	ne	17	0.13						
<i>Dimophyes arctica</i>	ne	15	0.11						
<i>Vogtia glabra</i>	ne	13	0.10						
<i>Sphaeronectes gracilis</i>	ne	12	0.09					2.57	3
<i>Sulculeolaria turgida</i>	ne	11	0.08			2.48	4		
<i>Rosacea plicata</i>	ne	10	0.07	2.40	3				
	eu	176							
<i>Amphicaryon acaule</i>	ne	7	0.05						
<i>Sulculeolaria monoica</i>	ne	7	0.05	2.02	2				
<i>Sulculeolaria quadrivalvis</i>	ne	5	0.04	1.76	2				
<i>Lensia meteori</i>	ne	3	0.02						
	eu	6							
Praya dubia	ne	3	0.02						

co, colonies; eu, eudoxid; la, larvae; ne, nectophore; SAAW, Subantarctic Water; STW, Subtropical Water.

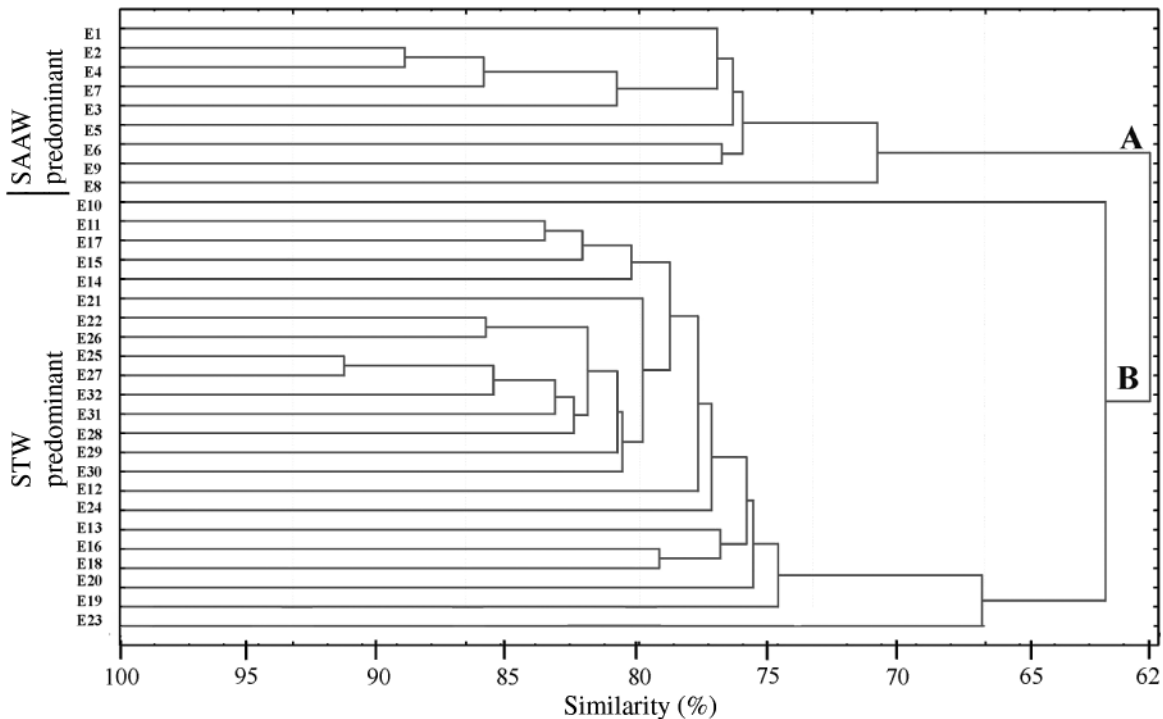


Fig. 4. Similarity dendrograms between the sampling stations. A: Coastal zone, B: Oceanic zone.

Peru–Chile Undercurrent (Silva and Neshyba, 1979; Strub *et al.*, 1998). In the coastal zone, this water mass is advected to the surface by upwelling, which fertilizes the surface layer and favors the high productivity of the HCS (Morales *et al.*, 1996; Daneri *et al.*, 2000; Silva and Valdenegro, 2003). As a corollary, these opposing productivity patterns could also create a natural boundary for secondary production, particularly for siphonophores, as the current study shows.

Of the 31 siphonophore species identified along the oceanic transect, 29 species had been previously reported off the Chilean coast, associated with the SAAW of the HCS (Ulloa *et al.*, 2000; Pagès *et al.*, 2001; Palma and Apablaza, 2004) or the STW around Easter Island (Palma, 1999); most of the previously recorded species are typical of epipelagic waters. A few isolated specimens of *L. multicristata*, *L. meteori*, *L. hotspur* and *V. glabra* were captured, possibly because of nictimeral displacements because these species have broad vertical distributions and also inhabit mesopelagic waters (Alvariño, 1971; Pugh, 1977; Ulloa *et al.*, 2000). Finally, *S. turgida* and *V. glabra* were captured and recorded for the first time in the eastern Central Pacific. Both the species are very scarce in the Pacific and had only been recorded in the westernmost zone (Alvariño, 1971). In general, we observed that the abundance of eudoxids and polygastric

phases of siphonophores followed the same patterns of geographic distribution in the transect between the Chilean coast and Easter Island.

Species richness increased from coastal to oceanic waters. The lowest species richness values (<10 species) were recorded at stations mainly associated with SAAW, where large aggregations of *M. atlantica*, *A. elegans* and *A. tetragona* (Group A species) were found. West of 76° W, greater species richness values were obtained, associated with STW. The elevated coastal abundance is supported by the high primary productivity associated with the HCS off northern Chile (Daneri *et al.*, 2000).

The high abundance of *M. atlantica* recorded at Station 8 probably resulted from enhanced population growth favored by the occurrence of a frontal zone between the SAAW and the STW. This speculation is supported by the fact that *M. atlantica* is a characteristic inhabitant of neritic waters in temperate zones (Alvariño, 1971; Pagès and Gili, 1992), is common in SAAW and is the predominant siphonophore along the entire Chilean coastline (20–55° S) (Palma and Apablaza, 2004; Palma and Silva, 2004). Furthermore, *M. atlantica* is particularly abundant in spring and summer and seems to be positively correlated with upwelling off Valparaíso (Palma and Rosales, 1995).

Most Group B species, associated largely with STW (Figs. 3 and 4), are common in the tropical–equatorial oceanic belt of the Pacific Ocean (Alvariño, 1971; Alvariño and Leira, 1986) and are also frequent in the warm waters of the Gulf of Mexico (Gasca, 1993). Furthermore, Group B encompassed transitional species and another distinctive group characterized by less abundant species found in the western zone of the study area (Fig. 3). It is interesting to note that, in both the groups, the predominant species were diphyids. Although this pattern could be a result of competition between families (i.e. diphyids versus abylopsyd), this speculation remains unconfirmed. However, it is important to underline that in the stations of the zone associated to SAAW, where the higher densities of eudoxid *A. tetragona* occurred, there was low occurrence of eudoxid *M. atlantica*. Such an opposite pattern, between the eudoxids of both the species, has also been found in other areas along the Chilean coast, where also the SAAW predominates (Palma and Rosales, 1995; Pagès *et al.*, 2001; Palma and Apablaza, 2004).

It is important to emphasize that *C. contorta*, occurring near Easter Island in the current study, has also been reported as the most abundant siphonophore in surface waters (Palma, 1999). These results agree with a previous study suggesting that *C. contorta* is an indicator of tropical water in the Atlantic, Pacific and Indian oceans (see Alvariño, 1971). In addition, *C. contorta* is one of the dominant species in the warm waters around the Galapagos Islands and in Hansa Bay, Papua New Guinea (Pagès *et al.*, 1989). Moreover, the abundance of this species was also associated with the 1983 El Niño event off the California peninsula (Gasca and Suárez, 1992). As a corollary, we suggest that *C. contorta* is an indicator of STW in the ESP.

The faunistic similarity among the stations near the coast (Figs 3 and 4), typified by the abundance of *M. atlantica*, *A. elegans* and *A. tetragona*, suggested that these species were strongly associated with SAAW in the HCS, and they did not proliferate in epipelagic ocean waters having subtropical characteristics. Consequently, these species can be used to indicate the westernmost HCS boundary off northern central Chile. This asseveration is strengthened by the fact that these species are distributed within the first 100-m depth and are strongly associated with SAAW off the central Chilean coast (Ulloa *et al.*, 2000).

The occurrence of species typical of oceanic waters with wider geographic distributions (i.e. *B. bassensis*, *E. spiralis* and *L. subtilis*) in HCS waters may indicate an intrusion of STW toward the coastal zone. Similarly, a high density of *B. bassensis* was recorded off northern Chile (22–24° S) in January during the 1997 El Niño

event (Pagès *et al.*, 2001). Therefore, the results of the current research are consistent with theories that suggest that small assemblages of planktonic species can be used to identify water masses or define their geographic boundaries.

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