

Mesozooplankton features in a frontal area off northern Patagonia (Argentina) during spring 1995 and 1998*

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SUMMARY: Hydrography and spatial patterns of mesozooplankton communities in a frontal area off northern Patagonian were investigated in spring 1995 and 1998. Differential wind/tidal relative forcing appeared to drive along-shelf variations in the physical structure of the front and hence, planktonic patterns. Approaching the northern border of the system, the conspicuous presence of *Oithona helgolandica*, cladocerans and appendicularians, and the low fecundities of calanoid copepods suggest that a high proportion of the primary production may be channelled through microheterotrophic processes. Towards the southern area, calanoids dominated over cyclopoids, 'large' species (*Drepanopus forcipatus*, *Calanoides* cf. *carinatus*) were abundant, and copepod fecundities were high and steady, suggesting that there may be a more classical-like herbivorous food web. *Paracalanus parvus* and *Ctenocalanus vanus* occurred over the whole system but seemed to be key species in mixed and weakly stratified waters. Copepods peaked in stratified waters away from the front itself, while the abundance of eggs and nauplii was highest in weakly stratified waters next to the front. Apparently, the general heating occurring over the region in spring 1998 strongly affected both the physical and biological structure of the system. Unlike in 1995, a massive bloom of gelatinous zooplankton took place in 1998 and a bloom of the phagotrophic dinoflagellate *Noctiluca* sp. occurred in the northern area. Co-occurring copepod populations were depressed and their reproductive patterns seemed to be highly disrupted. Present observations stress the significance of variable external forcing in driving satisfactory habitat conditions for juvenile fish in the area.

Key words: zooplankton, tidal front, food webs.

RESUMEN: CARACTERÍSTICAS DEL MESOZOOPLANCTON EN UN ÁREA FRONTAL DE PATAGONIA NORTE (ARGENTINA) DURANTE LA PRIMAVERA DE 1995 Y 1998. – Los patrones de distribución del mesozooplancton fueron estudiados en un área frontal ubicada en la plataforma continental norpatagónica (Argentina) durante las primaveras de 1995 y 1998. Las variaciones latitudinales en la intensidad relativa de los forzantes viento y marea serían responsables de las diferencias observadas a lo largo de la estructura física del sistema. Estas diferencias llevan a patrones de composición y distribución del plancton también diferentes. Hacia el norte, la conspicua presencia de *Oithona helgolandica*, cladóceros y apendicularios, y las bajas fecundidades de copépodos calanoideos que se registraron, sugieren que allí una alta proporción de la producción primaria podría estar siendo canalizada a través de procesos microheterotróficos. Hacia el extremo sur, en cambio, los copépodos calanoideos dominaron sobre los ciclopoideos, fueron abundantes especies relativamente 'grandes' (*Drepanopus forcipatus*, *Calanoides* cf. *carinatus*) y las fecundidades de copépodos fueron altas, sugiriendo allí la existencia de una trama trófica clásica, básicamente herbívora. Los copépodos *Paracalanus parvus* y *Ctenocalanus vanus* estuvieron presentes en toda el área de influencia del sistema, pero parecieron ser especies clave en aguas mezcladas y débilmente estratificadas. La abundancia de copepoditos y adultos fue máxima en aguas estratificadas lejos de la discontinuidad térmica, mientras que la de huevos y nauplii fue más alta en aguas estratificadas próximas al frente. Aparentemente, el calentamiento general que se pro-

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dujo en la región en 1998, afectó severamente las estructuras física y biológica del sistema. A diferencia de 1995, en la primavera de 1998 se registró un bloom masivo de zooplancton gelatinoso (ctenóforos), y en el área norte se produjo además otro del dinoflagelado fagotrófico *Noctiluca* sp. Paralelamente se observaron muy bajas densidades de copépodos y sus patrones reproductivos estuvieron seriamente alterados. Las características planctónicas diferenciales a lo largo del Sistema Frontal Norpatagónico se traducirían en oportunidades tróficas diversas para las larvas y juveniles de peces que se distribuyen en la región. Las presentes observaciones enfatizan la importancia de los forzantes físicos en la creación de condiciones adecuadas para la supervivencia de larvas y juveniles.

Palabras clave: zooplancton, frente de marea, redes tróficas.

INTRODUCTION

Hydrographic fronts are physically driven structures that highly influence ecosystem dynamics (e.g. Pingree *et al.*, 1978; Le Fèvre, 1986). They are at present largely recognized as areas of enhanced primary and secondary production, and thus often related to major fishing grounds on continental shelves of certain regions (e.g. North Sea -Daan *et al.*, 1990; Georges Bank -Sherman *et al.*, 1988). Interannual differences in external forcing are expected to affect frontal manifestation and hence, biological patterns.

The Patagonian shelf off Argentina is characterized by high tidal dissipation rates, which in nearshore waters generate a strong vertical mixing that may homogenize the whole water column. This feature, combined with the stratification of shelf waters induced by seasonal surface warming, leads to the occurrence during spring and summer of shelf sea fronts separating highly mixed coastal areas from stratified waters offshore. A major frontal zone is located near Peninsula Valdés (Fig. 1) extending southward along the Patagonian coast from ca. 42° to 45°S (Carreto *et al.*, 1986; Glorioso, 1987; Bakun and Parrish, 1991; Glorioso and Simpson, 1994; Glorioso and Flather, 1995; Guerrero and Piola, 1997; Sánchez *et al.*, 1998).

The tidal frontal system off northern Patagonia is associated with a highly productive shelf ecosystem. Reproductive strategies of two major fish resources, Patagonian anchovy *Engraulis anchoita* and Argentinian hake *Merluccius hubbsi*, appear to be closely linked to the dynamics of the system since main spawning and nursery areas of both species occur in the region (Ciechomski and Weiss, 1974a; Alheit *et al.*, 1991; Bakun and Parrish, 1991; Ehrlich and Ciechomski, 1994; Sánchez and Ciechomski, 1995; Sánchez *et al.*, 1998; Ehrlich, 1998). The system also seems to influence the distribution of adult stocks of those species (Podestá, 1989; Hansen *et al.*, 2001) and provide suitable thermal conditions for annual summer spawning of squid *Illex argenti-*

nus (Brunetti *et al.*, 1998). Largest concentrations of scallop *Chlamys patagonica* found in the region have also been related to the formation of the front (Orensanz *et al.*, 1991).

As in north-west European shelves (e.g. Le Fèvre, 1986), the northeastern U.S. (e.g. Anderson, 1997) and South African coast (e.g. Pitcher *et al.*, 1998), the frontal area off northern Patagonia is a place of occurrence of both harmful and unarmful red tides. Toxic outbreaks of paralytic shellfish poisoning of different intensity caused by the dinoflagellate *Alexandrium tamarense* have been recorded in relation to the frontal system since 1980 (Carreto *et al.*, 1981a, 1985, 1986, 1998). This occurrence initially prompted ecological research in the region, considering that the occurrence of the front was first detected in the area of Peninsula Valdés in relation to algal blooms. However, the plankton dynamics associated with the frontal system are still poorly understood. To date, zooplankton studies have addressed the distribution and abundance of different zooplankton groups (Alheit *et al.*, 1991; Viñas *et al.*, 1992; Santos, 1993; Mölemkamp, 1996; Mianzan and Guerrero, 2000), in relationship to both toxic and non-toxic phytoplankton blooms (Santos and Ramírez, 1995), as well as to food availability for first-feeding larvae of anchovy and hake (Viñas and Ramírez, 1996; Viñas and Santos, 2000). Some studies have suggested an uncoupled phyto-zooplankton relationship due to copepod exclusion and their replacement by the phagotrophic dinoflagellate *Polykrikos schwartzii* as the major predator, at least during some toxic booms (Carreto *et al.*, 1985, 1986; Santos and Ramírez, 1995). The absence of a short, herbivorous pathway would imply the cycling of organic matter through a microbial food web and/or sedimentation to the sea-floor, and thus an overall less efficient transfer of energy to higher trophic levels (*sensu* e.g. Cushing, 1989; Kiørboe, 1993). Even so, enhanced plankton production related to frontal dynamics appears to be the main reason for the occurrence of suitable feeding grounds favouring the accumulation of larval fish in the area

(Pájaro, 1989; Viñas and Ramírez, 1996; Clemensen *et al.*, 1997; Viñas and Santos, 2000).

In this study we explore the zooplankton patterns resulting from the changing biophysical conditions across the system, and the characteristics of the communities linked to along-shelf differences in the frontal features off northern Patagonia. We also examine the effects of varying frontal activity due to atmospheric forcing by comparing mesozooplankton features over two hydrographically different spring periods.

General description of the frontal system

The hydrographic structure of the system has been previously described by Carreto (1981, 1985, 1986), Glorioso (1987), Alheit *et al.*, (1991), Bakun and Parrish (1991) and more recently reviewed by Sánchez *et al.* (1998) and Hansen *et al.* (2001). In brief, the frontal system starts forming in spring as seasonal thermoclines develop in shelf waters offshore and persists until autumn when stratification declines. Highest stability of the system is reached in summer. In spring and summer, the temperature profiles across the front show a clear separation between the coastal area, characterized by well-mixed waters, and the offshore region, where a sharp thermocline of varying thickness at 20-40 m depth separates the upper and bottom waters. A transitional (frontal) area is defined by strong horizontal gradients as the thermocline intersects surface and bottom layers. The average position of the front can be adequately predicted by both Simpson-Hunter, $\log(h/w^3)$, and Simpson ϕ , parameters (Glorioso and Simpson, 1994; Sánchez *et al.*, 1998). Tidal currents, density fields and wind-driven circulation, the latter to a lesser extent, dominate the mean flow in the area. Direct current measurements indicate a mean flow parallel to the local isobaths, with increasing intensity seawards (Rivas, 1997).

The average position of the system estimated over the period 1984-1999 (Martos, unpublished data) shows an overall NE-SW alignment following closely that of the bathymetry (Fig. 1). Two major features between *ca.* 42°S and 45°S appear to rule frontal location. These are the differential dissipation rates occurring from north to south (Glorioso and Simpson, 1994; Glorioso and Flather, 1997; Glorioso, 2000), and the shifting of the 75-80 m isobath from a position over middle shelf to one near the coastline. The dissipation over most of the region is of the order of 0.1 W m^{-2} but it is highly

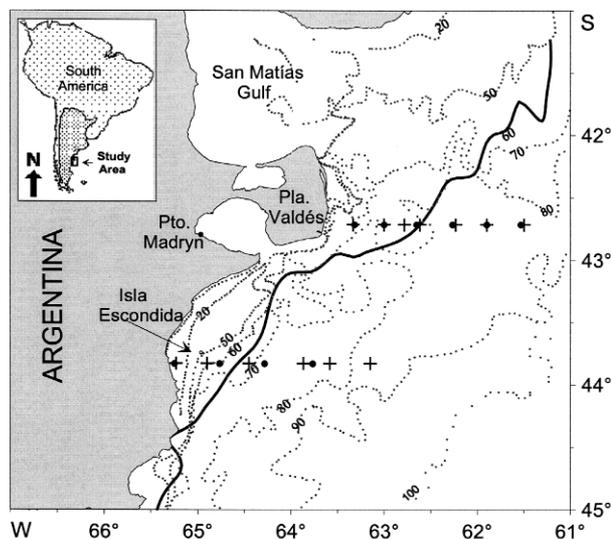


FIG. 1. – North Patagonian frontal system. Location of the study area showing major landmarks, average mean position of the front (estimated to coincide with a value of 40 J m^{-3} for the Simpson parameter ϕ), and position of the stations where zooplankton sampling was carried out in spring 1995 (●) and 1998 (+). The average location of the front was estimated from unpublished data collected over the period 1984-1999.

concentrated NE of Península Valdés, where maximum values exceed 50 W m^{-2} because of the coastline configuration (Glorioso and Simpson, 1994). Topographic shoals located SE and NE of Península Valdés also intensify tidal mixing (Glorioso, 1987). As a result, the front is located offshore in the northern area, on average 80 km from the coastline, and it approaches the shore southwards, positioning on average at 50 km from the coast.

MATERIALS AND METHODS

Sampling was carried out during two anchovy stock assessment surveys conducted in northern Patagonia in late spring 1995 (5-21 December) and 1998 (7-20 December). At all stations ($N=58$ in 1995, $N=60$ in 1998) depth profiles of temperature and salinity were measured with a Sea-Bird 19 CTD. Samples for calibration of the salinity data were taken at several depths covering the area and the temperature was calibrated by reversing thermometers. Stratification of the water column was estimated from the stability parameter ϕ (Simpson, 1981). A critical value of 40 J m^{-3} was considered to separate mixed from stratified waters (Martos and Sánchez, 1997).

Zooplankton sampling was specifically carried out along two transects (Fig. 1), each one crossing frontal areas characterized by different hydrograph-

ic conditions (see Results). These transects fitted the overall design of the cruises and therefore the full cross-frontal coverage of the whole system was not always possible, particularly in the northernmost area. At each station (N= 10 in 1995, N= 13 in 1998), samples for zooplankton enumeration were collected with a small Bongo net of 20 cm diameter and 150 μm mesh towed vertically from near the bottom to the surface. Sample water volume (4-6 m^3) was estimated by a General Oceanic mechanical flowmeter. Samples were preserved in 4% buffered formaldehyde solution. Zooplankton counting was performed in subsamples where at least 200 adult or C4-5 copepods were classified to species. Other zooplankton taxa occurring in the subsample were also enumerated. Normally a total of 700-1000 individuals were counted for each sample. It has to be pointed out that the counts of copepod eggs and nauplii were not accurate quantitative estimates of their abundance because they were not efficiently collected by the net (150 μm mesh) used for zooplankton sampling. However, these counts can be compared, and the differences between areas and situations can be shown.

Copepod egg production was estimated at a few stations from incubation of females of the dominant calanoid species. Live animals for experimental work on board were collected by lowering a 220 μm mesh net of 45 cm diameter to about 10 m depth. The net remained filtering in the water for 10 minutes while the ship drifted. Once on deck, the sample was immediately diluted in 15 l seawater, and then adult females were sorted to species for incubations. Females were placed in 500 or 1000 ml screw cap bottles containing 40 μm screened seawater. Five or six individuals of the smaller species or only a single individual of *Calanoides* cf. *carinatus* were kept per bottle. Copepods were incubated at *in situ* temperatures in a tub through which seawater pumped from 4 m depth was continuously circulating. After 24 h, the newly spawned eggs were collected onto a 40 μm mesh screen, and then they were either counted or preserved in Lugol's solution for later enumeration at the laboratory. It should be noted that the present fecundity estimates represent only conservative values since no replicates were made for most of the measurements due to logistical constraints on board.

The occurrence of jellyfish was particularly evident during mesozooplankton sampling in spring 1998. Because simultaneous quantitative sampling of gelatinous zooplankton had not been specifically

planned, abundance of jellyfish was roughly back-estimated from acoustic data collected at the time of the cruises. Acoustic interpretation was based on findings of a previous study, conducted in the same area and season, where a few gelatinous species (mainly *Mnemiopsis leidyi* and *Aequorea* sp.) were identified as responsible for creating typical echorecordings (Álvarez Colombo *et al.*, 2000). Hence, an Abundance Index was estimated from backscatter calculation by assuming that echo recordings of the same kind would be indicative of jellyfish species. Acoustic data were recorded with a Simrad EK500 scientific echosounder connected to a 38 kHz split-beam transducer. Sound scattering layer (SSL) of gelatinous zooplankton was detected at this frequency with a -70 dB threshold and each year the mean acoustic back-scattering energy by surface unit (s_a , $\text{m}^2 \text{nm}^{-2}$) was calculated for the entire water column across the two transects.

RESULTS

Hydrography and frontal structure along the system

Over the surveyed region, sea surface temperature increased in offshore direction while bottom values decreased. Longitudinal gradients, which are indicative of frontal location, were stronger at bottom than at surface in both years (Fig. 2). In 1998, both surface and bottom fields were warmer than in 1995. Much weaker gradients were observed at the surface in 1998. The distribution of salinity was similar in both years, showing a vertically homogeneous field that ranged from 33.5 to 33.9, with higher values occurring to the north (data not presented). The influence of warmer and more saline waters from San Matías Gulf (Guerrero and Piola, 1997) was apparent approaching the northern area of the front. Major along-shelf differences in the physical structure of the system can be summarized by comparing the vertical distributions of temperature through the cross-frontal sections off Peninsula Valdés (Fig. 3a and 5a) and off Isla Escondida (Fig. 4a and 6a). In the area off Península Valdés depth drops abruptly and there is almost no variation in depth along this section. The system shows a relatively wide unstratified sector and a rather extended transitional (frontal) one. Both surface and bottom signals of the front do not coincide spatially, with the bottom one stronger and displaced farther offshore. Because of

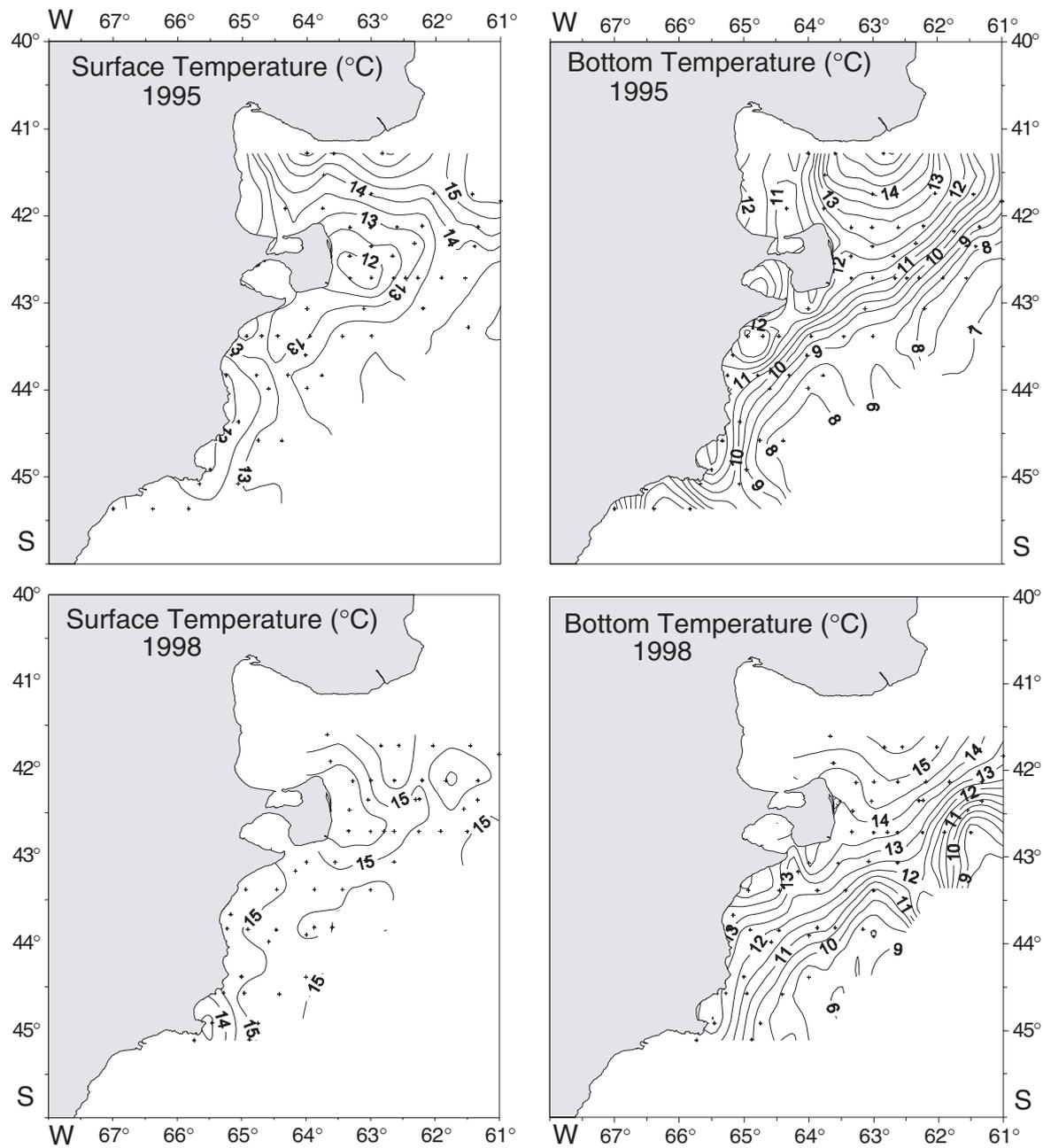


FIG. 2. – Sea surface and bottom temperature off northern Patagonia in spring 1995 and 1998.

the far distance from shore for the position of the front, a strongly stratified sector implying a near two-layered system, is not really evident along a 170 km transect. Off Isla Escondida, there is a gentle slope close to shore and depth increases gradually along this section. In this area, a very narrow mixed sector occurs (e.g. Fig. 4a), and both surface and bottom signals of the front concur spatially very close to shore, and a strongly stratified sector is well defined.

Hydrography and mesozooplankton features in spring 1995

Cross-frontal section off Peninsula Valdés

In this area, the mean position of the front was located at about 80 km from shore (Fig. 3a). A critical ϕ value of 40 J m^{-3} near St 740 separated vertically mixed isothermal waters (11.5°C) from thermally stratified ones (Fig. 3b). Strong surface ($\Delta T =$

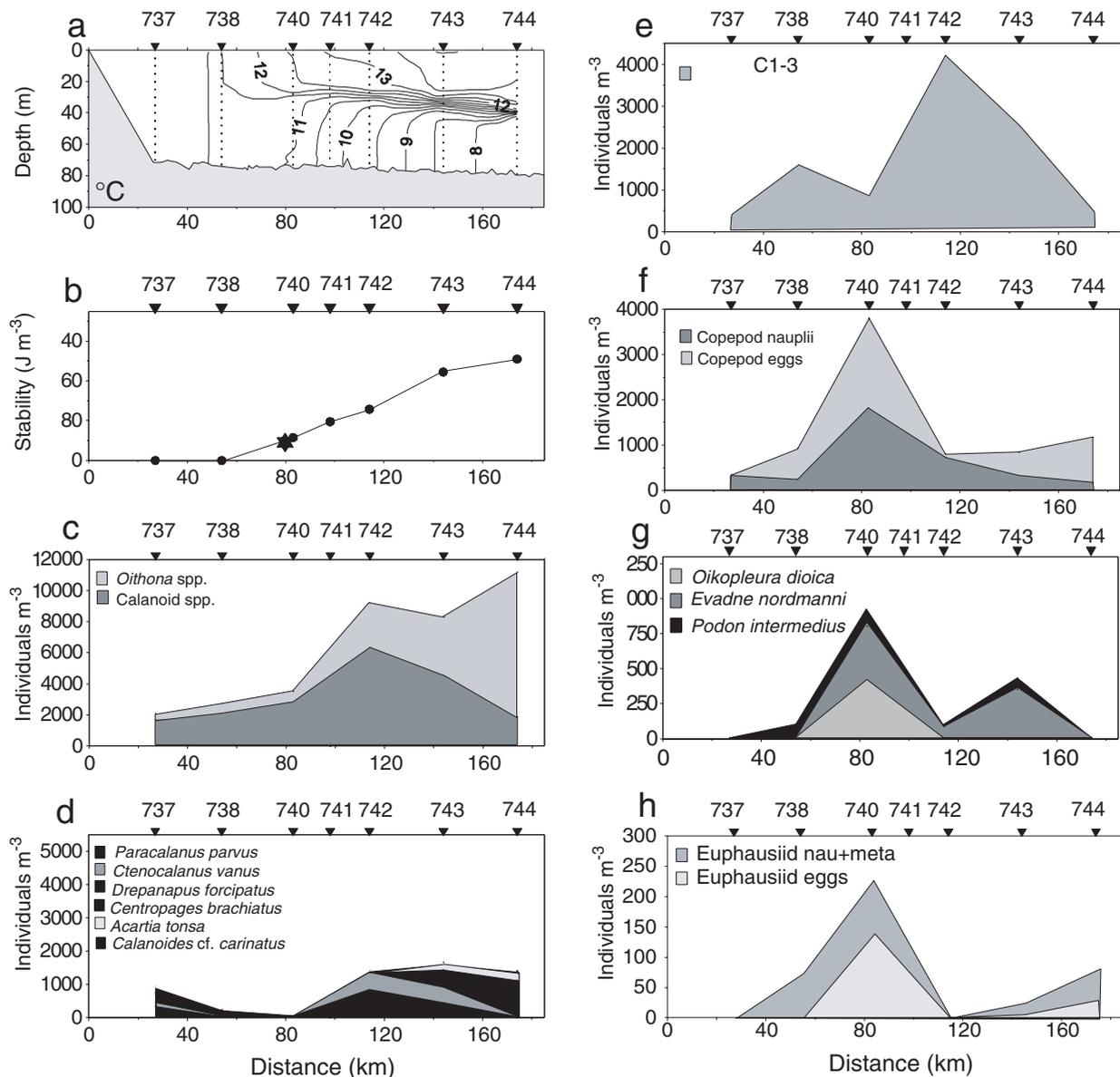


FIG. 3. – Spring 1995. Cross-frontal section off Península Valdés: (a) vertical distribution of temperature, °C, (b) stability parameter ϕ , location of the critical value is highlighted with a star symbol, (c) copepod distribution, ind m^{-3} , (d) species-specific C 4-6 abundance, (e) C 1-3 abundance (all the calanoid species pooled together), (f) abundance of copepod eggs and nauplii (note that the figures do not represent accurate quantitative estimates but only show trends - See text), (g) abundance of non-copepod zooplankton, and (h) abundance of eggs, nauplii and metanauplii of euphausiids.

0.27°C/10 km) and bottom ($\Delta T = 0.39$ °C/10 km) horizontal gradients created a wide transitional/frontal area of about 70 km. The bottom signal of the front was somewhat shifted offshore. A thick thermocline layer was located between 25-50 m ($\Delta T = 0.26$ °C/m).

In well-mixed coastal waters (St 737 and 738), abundance of all developmental stages of copepods was low (ca. 2000 ind m^{-3}) with calanoid species dominating (80%) over the cyclopoid *Oithona* spp. (Fig. 3c). *Paracalanus parvus*, *Drepanopus forcipatus*

and *Calanoides cf. carinatus* were the most abundant calanoids if stages older than C4 are considered (Fig. 3d). Concentrations of younger copepodids (C1-3) were relatively high (Fig. 3e) while those of eggs and nauplii were relatively much lower than in the transitional (frontal) area (Fig. 3f). Non-copepod mesozooplankton was represented by very low concentrations of the cladoceran *Podon intermedius* (Fig. 3g). Average (calanoids) copepod egg production rate was 9.2 ± 1.2 eggs $female^{-1} d^{-1}$, with higher fecundi-

ties realized by *Paracalanus parvus* and *Calanoides cf. carinatus* (Table 1).

In the transitional sector (St 740 to 743), abundance of copepods increased from weakly to more strongly stratified waters. Maximum values *ca.* 11,000 ind m⁻³ were reached offshore at St 744. Dominance of cyclopoids over calanoids gradually switched from 20% to 80% in coincidence with increasing stability of the water column (Fig. 3c). In weakly stratified waters calanoid copepods were dominated by *Paracalanus parvus* and *Ctenocalanus vanus* (60% and 25% on average, respectively), their numbers decreasing seawards. *Centropages brachiatus* and *Acartia tonsa* showed an opposite trend (Fig. 3d). The bulk of cyclopoids biomass recorded in waters with strong thermal stratification was exclusively built up of *Oithona helgolandica* (*sensu* Ramírez, 1966). Adult and younger calanoid copepodids (Fig. 3d-e) were higher in the more strongly stratified waters close to the front, while eggs and nauplii peaked at the front itself (St 740) (Fig. 3f). Mesozooplankton other than copepods, such as the cladoceran *Evadne nordmanni*, the appendicularian *Oikopleura dioica* and eggs, nauplii and metanauplii of euphausiids also peaked

in the vicinity of the front and decreased in the offshore direction. Numbers of *Evadne nordmanni* were much higher relative to *Podon intermedius*, and *Oikopleura dioica* did not occur at all, in waters with stronger stratification (Fig. 3g-h). Copepod egg production rates in strongly stratified waters were lower (5.7 eggs female⁻¹ d⁻¹) than those measured in the vertically isothermal coastal waters (Table 1).

Cross-frontal section off Isla Escondida

The front occurred very close to shore (*ca.* 20 km) in this area (Fig. 4a-b). The temperature profile across this section shows a remarkably narrow vertically homogeneous side (11.5°C), and also a narrow transitional sector extending through about only 20 km. Surface and bottom horizontal gradients were the same ($\Delta T = 0.55^\circ\text{C}/10\text{ km}$) and co-occurred spatially. Unlike the section off Peninsula Valdés, from St 768 onwards, the stratified sector of the system was clearly evident, characterized by the presence of well-mixed upper and bottom layers, where temperature was 13°C and 9°C respectively, separated by a thin thermocline ($\Delta T = 0.66^\circ\text{C}/\text{m}$) located at about 30 m.

TABLE 1. – Conservative estimates of *in situ* copepod egg production along two transects across the North Patagonian frontal system during spring 1995 and 1998.

Station	Temperature * (°C)	Species	N° of replicates	Fecundity (n° eggs fem ⁻¹ d ⁻¹)
Off Peninsula Valdés		Spring 1995		
St 737 Homogeneous Sector	12.5 / 14.0	<i>Calanoides cf. carinatus</i>	2	10.0
		<i>Paracalanus parvus</i>	1	10.0
		<i>Acartia tonsa</i>	1	7.5
		<i>Centropages brachiatus</i>	1	9.3
St 744 Stratified Sector	14.0 / 15.6	<i>Centropages brachiatus</i>	1	5.7
Off Isla Escondida				
St 766 Transitional Sector	12.5 / 14.3	<i>Acartia tonsa</i>	2	25.9
St 770 Stratified Sector	13 / 14.9	<i>Acartia tonsa</i>	1	19.7
Off Peninsula Valdés		Spring 1998		
St 752 Homogeneous Sector	14.0 / 16.0	<i>Calanoides cf. carinatus</i>	3	0
		<i>Paracalanus parvus</i>	2	0
Off Isla Escondida				
St 780 Stratified Sector	16.0 / 17.5	<i>Calanoides cf. carinatus</i>	2	0
		<i>Centropages brachiatus</i>	2	0
		<i>Acartia tonsa</i>	2	0
St 782 Stratified Sector	16.0 / 18.0	<i>Calanoides cf. carinatus</i>	1	7.5
		<i>Centropages brachiatus</i>	1	3.6
		<i>Acartia tonsa</i>	1	16.7

* Sea surface / Incubation temperature

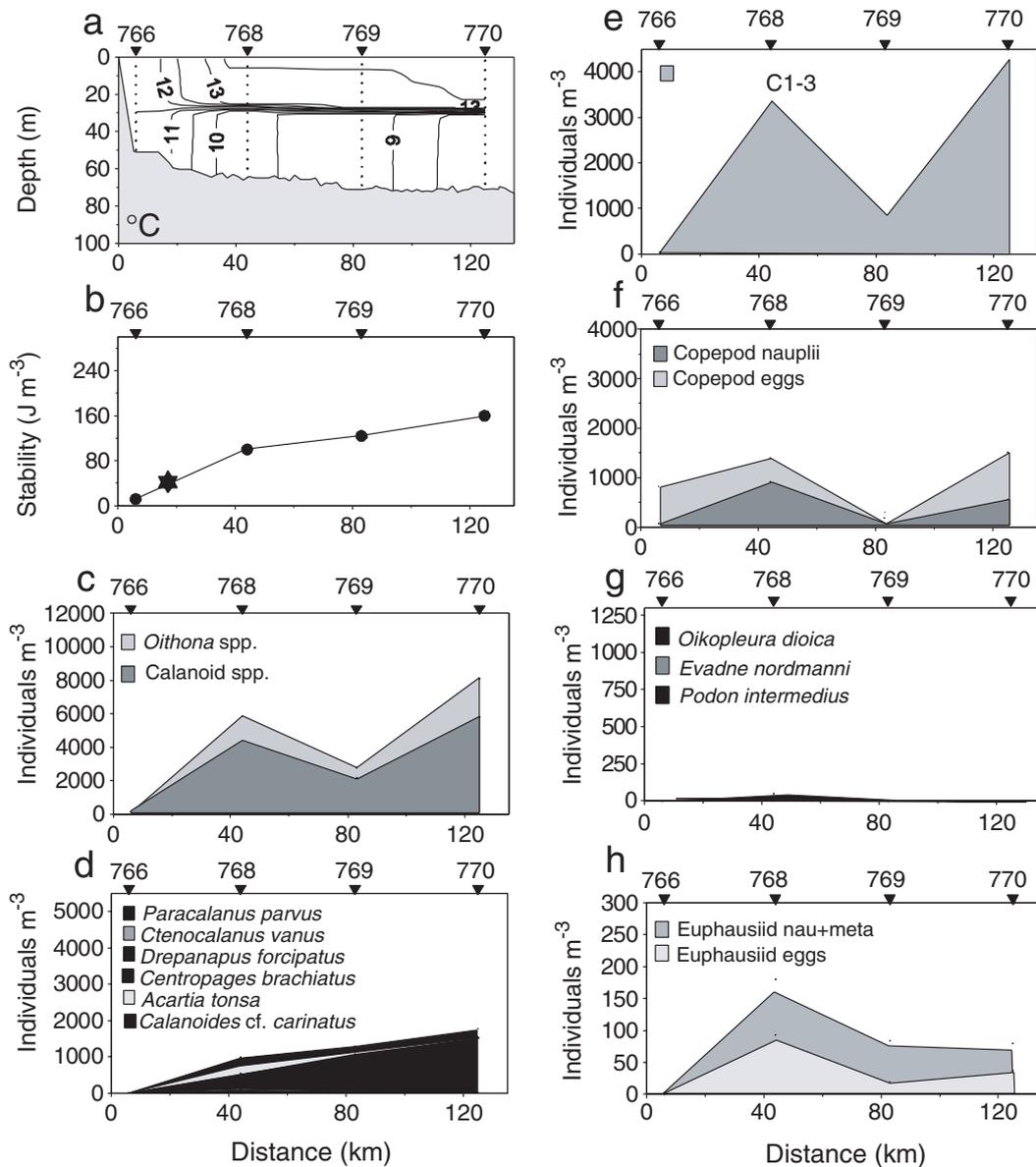


FIG. 4. – Spring 1995. Cross-frontal section off Isla Escondida: (a) vertical distribution of temperature, °C, (b) stability parameter ϕ , location of the critical value is highlighted with a star, (c) copepod distribution, ind m^{-3} , (d) species-specific C 4-6 abundance, (e) C 1-3 abundance (all the calanoid species pooled together), (f) abundance of copepod eggs and nauplii (note that the figures do not represent accurate quantitative estimates but only show trends – See text), (g) abundance of non-copepod zooplankton, and (h) abundance of eggs, nauplii and metanauplii of euphausiids. Notice that sampling resolution along this section was lower than off Península Valdés.

In the well-mixed coastal waters of this section (St 766), the lowest concentrations of total copepods of the whole cruise were recorded (*ca.* 150 ind m^{-3}). Almost exclusively calanoids were present (97%) with *Drepanopus forcipatus*, *Centropages brachiatus* and *Acartia tonsa* as dominant species. Nevertheless, relatively high numbers of eggs (*ca.* 1000 ind m^{-3}) were found, concurrent with the highest egg production rates (25.9 ± 0.5 eggs female $^{-1}$ d $^{-1}$ on average) measured throughout the survey (Table 1). Other mesozooplankton taxa distinct from copepods were absent (Fig. 4c-h).

Along this section, an overall trend of increasing copepod abundance from the less-stratified waters close to shore to those with a much stronger thermal stratification seawards was observed. In comparison with stratified waters off Península Valdés, concentrations did not vary appreciably but remained rather constant and high within the range *ca.* 6000 - 8000 ind m^{-3} . The same trend applies to eggs and nauplii of copepods. Specific composition changed from a rather diverse copepod community occurring in stratified waters close to the front itself, where *Drepanopus forcipatus*

(32%), *Centropages brachiatus* (26%) and *Acartia tonsa* (20%) shared dominance, to one widely dominated by *Drepanopus forcipatus* (80%) followed by *Calanoides cf. carinatus*. Unlike in stratified waters off Península Valdés, *Oithona helgolandica* was recorded in very low numbers along this transect. Relatively high copepod fecundities (19.7 eggs female⁻¹ d⁻¹) were also measured in strongly stratified waters (Table 1). Non-copepod mesozooplankton was much less abundant than off Península Valdés. Relatively higher concentrations of *Podon intermedius* and eggs, nauplii and metanauplii of euphausiids were recorded in stratified waters near the transitional sector. The tunicate *Oikopleura dioica* was not present in this area (Fig. 4c-h).

Hydrography and mesozooplankton features in spring 1998

Cross-frontal section off Península Valdés

The frontal signal at the surface was extremely weak (0.17°C/10 km) compared to 1995. The bottom gradient was much stronger (0.78°C/10 km) and displaced offshore (Fig. 5a). The front was located at approximately 90 km from the coast, and it marked the limit of coastal isothermal waters (14°C). A broad transitional sector was apparent seaward at St 755 and was maintained until the end of the transect. A seasonal thermocline ($\Delta T = 0.34^\circ\text{C}/\text{m}$) was present offshore between 40-60 m, this time deeper than in 1995. A temporary thermo-

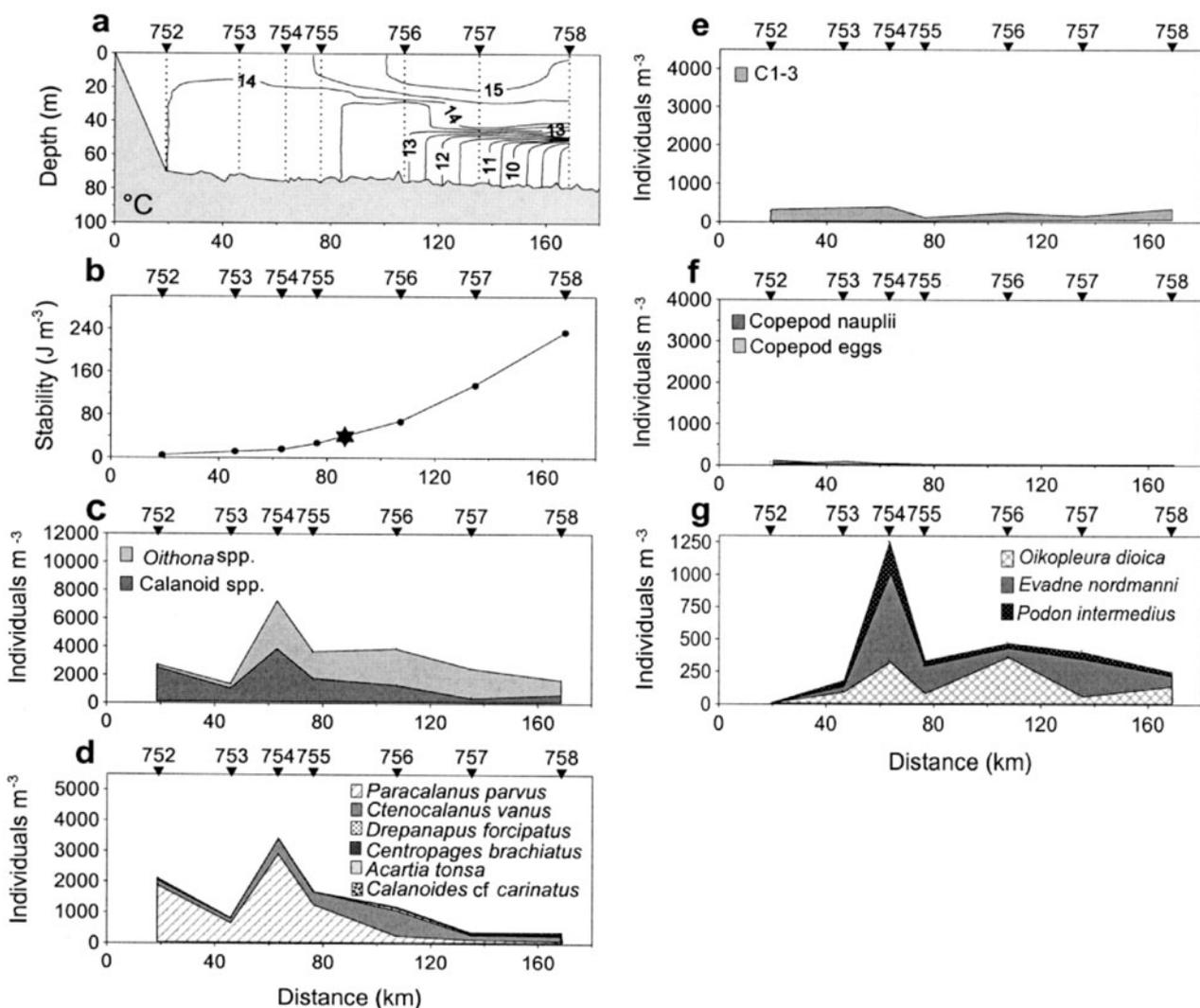


FIG. 5. – Spring 1998. Cross-frontal section off Península Valdés: (a) vertical distribution of temperature, °C, (b) stability parameter ϕ , location of the critical value is highlighted with a star, (c) copepod distribution, ind m⁻³, (d) species-specific C 4-6 abundance, (e) C 1-3 abundance (all the calanoid species pooled together), (f) abundance of copepod eggs and nauplii (note that the figures do not represent accurate quantitative estimates but only show trends – See text), and (g) abundance of non-copepod zooplankton.

cline was also formed in the upper layer at *ca.* 20 m depth (Fig. 5a-b).

In relatively well-mixed and weakly-stratified waters close to shore (St 752 to 755), copepod abundance was *ca.* 2000 ind m⁻³ at the most coastal stations, and peaked in weakly-stratified waters next to the transitional sector (*ca.* 8000 ind m⁻³ at St 754). Dominance of calanoid species comprising 80-90% of total numbers in coastal waters switched to oithonids from St 754 seawards, increasing with stronger stratification (Fig. 5c). *Paracalanus parvus* vastly outnumbered any other calanoid species (on average 85% of total calanoids), their abundance decreasing offshore, followed by *Ctenocalanus vanus* (Fig. 5d). Younger developmental stages of copepods were scarce (Fig. 5e) and the approximate abundance of copepod eggs and nauplii was also low (Fig. 5f). Non-copepod mesozooplankton also

peaked in waters with weak stratification next to the transitional area. The peak was comprised of *Evadne nordmanni*, *Oikopleura dioica* and low numbers of *Podon intermedius* (Fig. 5g). There was no egg production during experiments conducted at St 752 with *Paracalanus parvus* and *Calanoides cf. carinatus* (Table 1).

In the transitional/frontal area (St 756 to 758), the number of total copepods remained fairly constant (*ca.* 3000 - 4000 ind m⁻³), decreasing slightly in the offshore direction. Oithonids dominated over calanoid species, of which *Ctenocalanus vanus* and *Paracalanus parvus* comprised on average 50% and 25% of total calanoids, respectively. *Drepanopus forcipatus* was also present but in very low concentrations. Abundance of copepod stages younger than C3 was as scarce as in isothermal or less-stratified coastal waters. Concentrations of mesozoo-

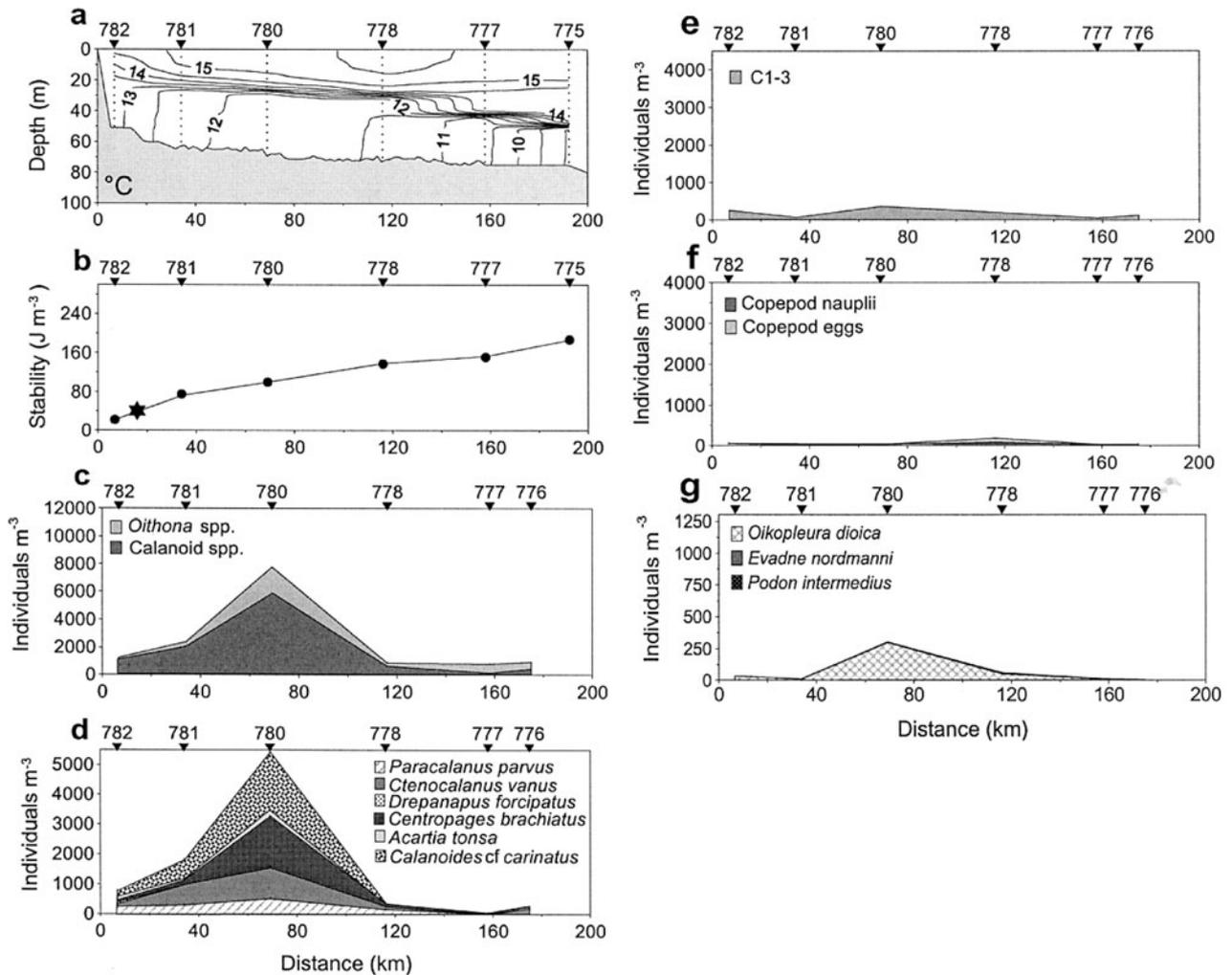


FIG. 6. – Spring 1998. Cross-frontal section off Isla Escondida: (a) vertical distribution of temperature, °C, (b) stability parameter ϕ , location of the critical value is highlighted with a star, (c) copepod distribution, ind m⁻³, (d) species-specific C 4-6 abundance, (e) C 1-3 abundance (all the calanoid species pooled together), (f) abundance of copepod eggs and nauplii note that the figures do not represent accurate quantitative estimates but only show trends –See text), and (g) abundance of non-copepod zooplankton.

plankton other than copepods did not vary much as stratification increased seawards, with *Oikopleura dioica* and *Evadne nordmanni* alternating in dominance, and *Podon intermedius* occurring in low numbers. Unlike in summer 1995, the heterotrophic dinoflagellate *Noctiluca* sp. was present throughout the entire transect off this area. Although they could not be properly quantified, high numbers were noticeable in the samples during zooplankton counting. *Noctiluca* sp. was apparently more abundant in the transitional area than on the coastal side of the system.

Cross-frontal section off Isla Escondida

Waters were stratified along the entire section (15 and 12°C in surface and bottom layers, respectively). This time, the critical ϕ value which was observed

very close to shore (*ca.* 20 km) resulted from the temperature gradient created only at the bottom ($\Delta T = 0.27^\circ\text{C}/10\text{ km}$) considering that the front did not show any signal at surface, and actually separated adjacent areas that were both stratified but at different rates. Therefore, St 782 and 781 were located in the transitional/(bottom)frontal area, while from near St 780 seawards a strongly stratified sector was apparent. Both temporary and seasonal thermoclines were present at 20 m ($\Delta T = 0.21^\circ\text{C}/\text{m}$) and 40-60 m ($\Delta T = 0.45^\circ\text{C}/\text{m}$) depth, respectively (Fig. 6a-b). The temperature gradient observed near the bottom approaching the end of the transect is indicative of mid-shelf waters flowing SW-NE. These waters were not detected off Península Valdés because they flow farther offshore. Besides, their occurrence was recorded off Isla Escondida only in 1998 because the transect carried out then was longer than in 1995.

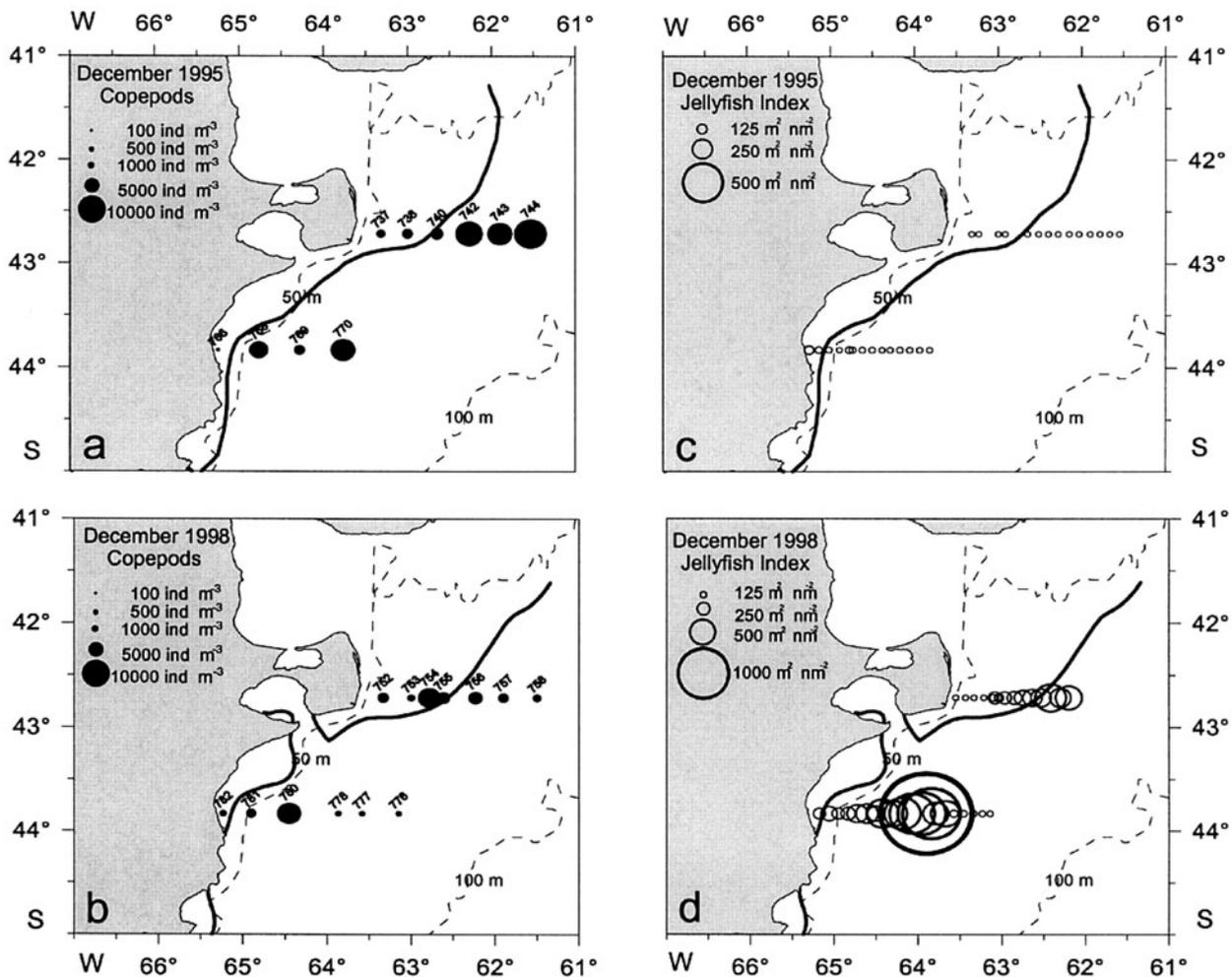


FIG. 7. – Copepod abundance (ind m^{-3}) and Jellyfish Index (mean acoustic back-scattering energy by surface unit, s_a , $\text{m}^2 \text{nm}^{-2}$) along the cross-frontal sections off Península Valdés and Isla Escondida in spring 1995 (a, c) and spring 1998 (b, d). The biomass of gelatinous zooplankton was roughly back-estimated from available acoustic data (see text). Mean position of the front ($\phi = 40 \text{ J m}^{-3}$) is also shown for both years.

Total copepod abundance was *ca.* 2000 ind m⁻³ in coastal weakly-stratified waters located above the temperature bottom gradient. Abundance peaked at St 782, in waters with stronger stratification, but still in the vicinity of the transitional/(bottom)frontal area. Oithonids were much less-abundant than off Península Valdés, so that calanoids were dominant along the entire section comprising on average 90% of total numbers (Fig. 6c). Among calanoids, *Ctenocalanus vanus* and *Paracalanus parvus* were always present, although with varying concentrations, while *Calanoides cf. carinatus*, *Centropages brachiatus* and *Acartia tonsa* occurred in the coastal transitional area disappearing offshore. Unlike in summer 1995, *Drepanopus forcipatus* was only occasionally present in low concentrations at the outermost stations (Fig. 6d). Similar to the area off Peninsula Valdés, off Isla Escondida the abundance of copepods younger than C3 (Fig. 6e) and the estimates of copepod eggs and nauplii were very low (Fig. 6f). Other than copepods, only the tunicate *Oikopleura dioica* was present and its abundance peaked at St 780 otherwise showing low abundance (Fig. 6g). Average calanoid fecundity measured in the coastal frontal area (St 782) was 9.2 ± 6.7 eggs female⁻¹ d⁻¹. Incubations with animals collected at St 780, concurrent with maximum total copepod abundance, yielded no egg production (Table 1).

The two distinct horizontal patterns of copepod abundance found in spring 1995 and 1998 across the frontal system off Northern Patagonia are summarized in Fig. 7a-b. Interestingly, in 1995 the abundance of gelatinous zooplankton was consistently low in both areas whereas the lower copepod concentrations observed in 1998 closely paralleled the occurrence of much larger jellyfish aggregations (Fig. 7c-d -Álvarez Colombo, unpublished data). In 1998 gelatinous biomass off Península Valdés, mostly comprised of the ctenophore *Mnemiopsis leidyi*, was relatively higher in offshore waters. Ctenophore occurrence at high concentrations, along with high abundance of the heterotrophic dinoflagellate *Noctiluca* sp., was particularly evident during sampling for fecundity assays in this area. All the experiments attempted in the transitional sector of the system failed, or could not be conducted at all, because gelatinous individuals entering the net seriously damaged copepods. Off Isla Escondida, relatively higher biomass of gelatinous zooplankton was regularly found along the entire section, peaking also in offshore waters.

DISCUSSION

Spatial patterns of plankton communities

The distribution of total mesozooplankton abundance across the North Patagonian frontal system in 1995 was similar in the northern and southern sections and it may represent the regular abundance pattern crossing the front. This resembles the typical pattern across tidal fronts occurring over the shelves of western Europe, where copepod biomass peaks in stratified waters away from the thermal discontinuity, while the abundance of copepod eggs and nauplii peaks in weakly-stratified waters close to the front, usually concurrent with maximum phytoplankton production and biomass (e.g. Holligan *et al.*, 1984; Kiørboe, 1993). Viñas and Ramírez (1996) have also previously reported eggs and nauplii of copepods peaking in frontal waters off Península Valdés at highest chlorophyll *a* concentrations. Correspondingly, our few measurements of calanoid egg production rates, though conservative, followed closely the trend found in frontal areas of the North Sea, with higher values occurring in mixed and transitional waters (Kiørboe and Johansen, 1986; Kiørboe *et al.*, 1988).

All the copepod species occurring in the area are typically distributed in cold coastal waters along Argentina (Ramírez and Bjönberg, 1981; Ramírez, 1981) and have been reported previously in relation to the frontal system off northern Patagonia (Santos and Ramírez, 1995; Mölemkamp, 1996; Santos, 1993). In accordance with Santos and Ramírez (1995), we found no particular copepod assemblages defining each sector of the system. However, *Paracalanus parvus* and *Ctenocalanus vanus*, although widely distributed over the whole area in both spring periods, appear to be key species for distinguishing mixed and weakly stratified waters. A striking difference in species composition between the northern and southern edges of the system, regardless of the year, was the much higher abundance of *Oithona helgolandica* in stratified waters off Península Valdés. Conversely, *Drepanopus forcipatus* prevailed offshore in the area of Isla Escondida, particularly in 1995. *Calanoides cf. carinatus* was also relatively much more abundant over the latter area in both years.

Non-copepod mesozooplankton such as cladocerans and appendicularians are also very common in frontal convergences and can reach in some cases high numbers (Le Fèvre, 1986). This is in good

agreement with our findings, primarily off Península Valdés, where *Podon intermedius*, *Evadne nordmanni* and *Oikopleura dioica* peaked in the vicinity of the front. Conversely, they were absent or were recorded in very low concentrations along the southern section. Both cladoceran species occur largely in the area (Ramírez and Pérez Seijas, 1985; Viñas *et al.*, 1992) and have been mentioned before as peaking in transitional waters off Valdés, the former being typically more abundant on the mixed side of the front and the latter on the stratified one (Mölemkamp, 1996; Santos, 1993). *Oikopleura dioica* is a coastal species widely distributed over the Argentine Sea (Esnal, 1981) that occurs at high concentrations in the study area (Capitanio *et al.*, 1997).

Differential wind/tidal relative forcing along the North Patagonian frontal system may account for the dissimilar physical settings that we observed approaching either the northern (Península Valdés) or southern (Isla Escondida) borders regardless of the year. Preliminary evidence illustrating major differences indicates that in the northern area the tidal flow is largely influenced by the coastline configuration and, in spring and summer, by prevailing northerly and southerly winds of 17-20 km h⁻¹ (Punta Delgada, period 1959-1968, Servicio Meteorológico Nacional, 1985). Although in the southern area the energy input by tides is lower, stronger prevailing south-west and westerly winds (25-30 km h⁻¹) occur during the warm season (Servicio Meteorológico Nacional, 2000). These latter winds may favour the retention of zooplankton in coastal waters by intensifying the overall Ekman transport directed onshore, thereby reinforcing the density-driven surface water flow toward the convergent front (*sensu* Bakun and Parrish, 1991, Fig. 8c). At the same time, this increased shoreward Ekman transport may enhance enrichment processes in the southern area by carrying onto the inner shelf nutrient-rich waters upwelled at the shelf-break. In support of this view, a sharp increase in the surface concentration of nitrates actually takes place at *ca.* 120 km from shore during spring and summer (Carreto *et al.*, 1981b, Fig. 9a).

It is apparent that in addition to the mesozooplankton pattern resulting from cross-frontal environmental heterogeneity, the different physical environment characterizing the northern and southern boundaries of the tidal front led to the occurrence of distinct plankton assemblages. The conspicuous presence of *Oithona helgolandica*, cladocerans and appendicularians, and the relatively

lower fecundities actually realized by calanoid copepods off Península Valdés suggests that in the northern area a high proportion of matter and energy transfer may be being channelled through a microheterotrophic food web. In fact, the sibling species *Oithona similis* has been frequently associated with microbial-based production (Franz and González, 1995; Nielsen and Sabatini, 1996; Nakamura and Turner, 1997). Because of its ability to feed mainly upon > 10 µm ciliates and heterotrophic (dino)flagellates this small-sized copepod could reintegrate microprotozooplankton production into more classical trophic pathways (Nakamura and Turner, 1997). Interestingly, Carreto *et al.* (1985) highlighted the dominance of *Oithona helgolandica* in relation to the 1981 toxic bloom caused by the dinoflagellate *Alexandrium tamarense*. Cladocerans and appendicularians would play a similar role as retrievers of primary production by grazing on small particles, down to bacteria size (e.g. Le Fèvre, 1986). We have no simultaneous data on either nutrients or phytoplankton and small-sized zooplankton. Nevertheless, current knowledge on nutrient and phytoplankton communities off Península Valdés (Carreto and Benavides, 1990; Alheit *et al.*, 1991) supports our hypothesis. In brief, the availability of nitrate is greater on the mixed side of the front compared to the euphotic zone in stratified waters where the largest nitrate concentrations occur in the bottom layer. There is a high interannual variability in phytoplankton composition which strongly influences the distribution and abundance of the patches. These two latter variables appear to be strongly dependent on the occurring species. Chlorophyll *a* usually peaks in the transitional/frontal area between well-mixed and well-stratified waters. On the mixed side of the system, detritus and chain-forming diatoms are dominant, in the transitional area autotrophic dinoflagellates predominate, and in the stratified sector heterotrophic dinoflagellates are most abundant. Further support for our hypothesis is given by the fact that coastal waters off Península Valdés along 70 km from shore can become strongly stratified as early as November and are dominated by microflagellates and coccal cells, which are typical components of systems based on regenerated production (Negri, 1994).

In contrast, environmental conditions seem to be more advantageous for calanoid copepods in the southern area, suggesting that a more classical herbivorous food web occurs, characterized by large

phytoplankton cells and the dominance of 'large' (calanoid) copepods, with a higher percentage of new production. Mesozooplankton and, particularly, copepod species composition in this area supports this suggestion. In addition to the overall dominance of calanoid species, *Calanoides* cf. *carinatus*, which has been typically associated with large-cell-dominated (= diatom) upwelling events (e.g. Walker and Peterson, 1991; Lopes *et al.*, 1999) was relatively much more abundant over this area in both years. The same was the case of *Drepanopus forcipatus*, which in 1995 was overwhelming dominant. To our knowledge there is no information on feeding requirements and environmental preferences of this species, but reproduction of the closely-related species *Drepanopus pectinatus* seems to be strongly dependent on high concentrations of phytoplankton (Alonzo *et al.*, 2001). Santos (1993) also reported high numbers of both species off Isla Escondida. Furthermore, *in situ* (calanoid) fecundity rates were comparatively much higher and steady in the southern area, denoting a more suitable food climate for those copepods. Limited information on phytoplankton biomass and composition in this area (Carreto *et al.*, 1981b; Lutz, unpublished data) indicates a strong dominance of diatoms over dinoflagellates and higher chlorophyll *a* concentrations ($> 4.0 \text{ mg m}^{-3}$) in waters off Isla Escondida than in the northern area off Península Valdés.

To summarize, the overall coupling between zoo- and phytoplankton would be much weaker approaching the northern area of the system, where primary production may have a large component of regenerated production. Stratification may therefore be intensified as a result of the broadening of the shelf, favouring the widespread and persistent development of dinoflagellate populations and the predominance of heterotrophic processes. Conversely, physical forcing acting over the southern area may thereby enhance the supply of nutrients, so that a rather classical herbivorous food chain, mainly based on new production, may prevail. This view is still speculative and mostly prompted by circumstantial evidence, but it provides a basis for further investigation. In any event, interannual variability in the blooming species of phytoplankton and the magnitude of their patches must play a major role in driving the structure of the (meso)zooplankton communities and further trophic pathways.

Studies in frontal regions of the North Sea have identified distinct plankton communities characterizing different hydrographic features, which seem to

strongly affect the pathways to higher trophic levels (e.g. Kiørboe *et al.*, 1988; Nielsen *et al.*, 1993; Richardson *et al.*, 1998). Thus, support is increasing for the hypothesis that larval nursery areas are somehow linked to frontal features (e.g. Munk *et al.*, 1999). Also, spatial variation in both species and size composition, as well as in abundance of copepods, have been shown to influence the species/size composition of associated fish larvae communities (e.g. Nielsen and Munk, 1998). Accordingly, and concurrent with the mesozooplankton patterns we found, there also seems to be a sort of geographical partitioning of the North Patagonian system in regard to the reproductive strategies of hake and anchovy. Whereas anchovy larvae are spread throughout the system in summer (Sánchez and Ciechowski, 1995), hake larvae concentrate in the area off Isla Escondida and southwards (Ehrlich, 1998). Findings by Viñas and Santos (2000) on first feeding of hake larvae also suggest that they could take advantage of the large-sized prey found in the southern area. Small-sized feeding items prevailing in the northern area may constitute more suitable conditions for food preferences and growth of anchovy larvae (Viñas and Ramírez, 1996; Clemmensen *et al.*, 1997). Therefore, *Oithona* populations may constitute the bulk of currently available prey for early anchovy. Coincidentally, the potential role of e.g. *Oithona similis* as a key link between small protozooplankton and fish larvae has been particularly emphasized in areas and/or seasons which are disadvantageous for calanoid copepods (Nielsen and Sabatini, 1996; Nakamura and Turner, 1997).

Interannual differences

The most remarkable physical difference between the two spring periods was the fact that in 1998 the whole system was much warmer (2°C) than in 1995 (Fig. 2). Actually, significant positive thermal anomalies in the water column, estimated over the period 1984-1999, were taking place in spring 1998 (Table 2). This general warming was likely responsible for the major interannual differences observed in the structure of the system. As a result, in 1998 the front was less prominent, mainly limited to a bottom phenomenon. Such conditions did in turn affect the structure of plankton communities. As compared with 1995, outstanding differences were the massive bloom of gelatinous zooplankton that took place in 1998, and the occurrence of a bloom of *Noctiluca* sp., though this latter was

TABLE 2. – Mean temperatures (°C) and thermal anomalies observed over the frontal system off northern Patagonia in summer 1995 and 1998. Thermal anomalies were calculated from *in situ* CTD measurements gathered from 1984 to 1999 (Martos, unpublished data). Average values refer to means estimated for the entire period.

Sector	1995		1998		Average
	Mean	Anomaly	Mean	Anomaly	
Mixed	12.25	- 0.69	14.16	+ 1.21	12.94
Stratified upper	13.48	- 0.99	15.47	+ 1.00	14.47
Stratified bottom	8.49	- 0.87	10.64	+ 1.28	9.36

only in the northern area. Co-occurring copepod populations were overall depressed and their reproductive patterns seemed to be highly disrupted. Actually, our egg production experiments suggest that by then copepods may be normally reproducing only in coastal waters off Isla Escondida, at relatively lower concentrations of ctenophores and where no evidence of any *Noctiluca* patch was apparent. In addition, young copepod stages that may be indicative of recent reproduction, were scarce along both sections. The phagotrophic dinoflagellate *Noctiluca* can become highly abundant at frontal convergences (Le Fevre, 1986). It has been shown that both food competition (Le Fevre and Grall, 1970), but mainly predation by this species on copepod eggs (Daan, 1987), can at times be of crucial importance in limiting growth of local copepod populations. On the other hand, the predation impact of (ctenophores) gelatinous zooplankton on copepods is largely known (Waggett and Costello, 1999 and references therein). When highly abundant, lobate ctenophores *Mnemiopsis* spp. may cause copepod populations to plummet in such a way that dominant species can even disappear for some time (Sullivan and Van Keuren, 2001). The distribution patterns of jellyfish biomass we found are in good agreement with previous findings that indicate large aggregations of mainly *Mnemiopsis leidyi* in relation to transitional and stratified waters off Península Valdés (Mianzan and Guerrero, 2000), although much higher concentrations of this species are recorded in the southern area (Alheit *et al.*, 1991). The latter pattern may be related to the prevalence of either cyclopoid or calanoid copepods in the northern and southern areas, respectively. Field studies on prey selection by *Mnemiopsis* spp. have demonstrated a positive selection for calanoids (*Acartia tonsa*) relative to cyclopoids (*Oithona colcarva*) that seem to result from differential encounter rates with alternative prey, which in turn depend on copepod swimming.

At similar prey concentrations, higher rates were found for the more actively-swimming *Acartia* than for the less-active *Oithona* (Costello *et al.*, 1999). Therefore, in terms of food, the northern *Oithona*-dominated area off Península Valdés may constitute a less favourable environment for the occurrence of adult *Mnemiopsis* than the southern calanoid-dominated area off Isla Escondida. If this is the case, when large populations of jellyfish aggregate in relation to the tidal system, hake larvae concentrated to the south may be exposed to a higher predation risk than early anchovy distributed over the northern area. As previously reported from data collected in December 1989 (Mianzan and Guerrero, 2000), the relatively low jellyfish biomass occurring in December 1995 may correspond to the first spring stage in the development of local ctenophore populations. Much higher values could be expected shortly after as growth proceeds. Hence, the remarkably higher gelatinous biomass we found in December 1998 relative to spring 1995 may represent a more advanced stage in the evolution of the populations in correlation with ‘earlier’ high temperatures, but also a population explosion that was most likely triggered by the unusual warming of the system. In accordance with this assumption, the seasonal pattern of northern populations of *Mnemiopsis leidyi* in US coastal waters appear to be strongly influenced by temperature, with short but intense blooms occurring in late summer and early fall (Kremer, 1994). Furthermore, recent studies have documented early spring appearances of this species that correlate with a climatic warming trend (Sullivan *et al.*, 2001).

CONCLUSIONS

In addition to the cross-frontal pattern of mesozooplankton abundance linked to the environmental heterogeneity across the North Patagonian frontal system, there were marked along-frontal differences in the composition and structure of the communities regardless of the year being considered. These differences were related to the dissimilar physical settings approaching either the northern or southern boundaries of the system, which in turn appear to obey to varying external forcing (tidal dissipation/winds).

Unlike in spring 1995, a massive bloom of gelatinous zooplankton and a bloom of *Noctiluca* sp. took place in 1998. Co-occurring mesozooplankton populations were depressed and their regular patterns

highly disrupted. These striking interannual differences likely resulted of the unusual warming of the system in 1998.

Although based on a limited data set, present observations in the North Patagonian tidal front emphasize the importance of variable physical forcing in determining year-to-year cross- and along-frontal distribution patterns of zooplankton communities, and hence pelagic food webs. We suggest that mesoscale (few months/few years) variations in atmospheric forcing may strongly affect juvenile fish distributed in the region, by alternatively changing favourable feeding and growth conditions into sites of high predation risk and competition for food.

Two major topics emerge as progress for the present study, both of them deserving further examination: (i) the dissimilarity of planktonic food web structures in relation to frontal activity and their influence on larval fish life; and (ii) the combined effects of long-term forcing (e.g. sea-air heat fluxes), and local wind-forcing in establishing frontal characteristics and coupled biological responses.

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REFERENCES

- Alheit, J., J. Ciechowski, L. Diurfeldt, C. Ebel, M. Ehrlich, J. Elgue, G. Mantero, Y. Matsuura, H. Mianzan, W. Nellen, C. Odebrecht, F. Ramírez, R. Sánchez, G. Shaffer and M.D. Viñas. – 1991. SARP studies on the Southwest Atlantic Anchovy, *Engraulis anchoita* off Argentina, Uruguay and Brazil. *ICES, Session V*, C.M. 1991/L:46, 32 pp.
- Alonzo, F., P. Mayzaud and S. Razouls. – 2001. Egg production and energy storage in relation to feeding conditions in the subantarctic calanoid copepod *Drepanopus pectinatus*: an experimental study of the reproductive strategy. *Mar. Ecol. Prog. Ser.*, 209: 231-242.
- Álvarez Colombo, G.L., H.W. Mianzan and A. Madirolas. – 2000. Caracterización acústica de la estructura espacial de las agregaciones norpatagónicas del ctenóforo *Mnemiopsis leidyi* y de la hidromedusa *Aequorea* sp. 15° *Simposio Científico Tecnológico Comisión Técnica Mixta del Frente Marítimo*, Mar del Plata, 22-24 Noviembre 2000. POSTER.
- Anderson, D.M. – 1997. Bloom dynamics of toxic *Alexandrium* species in the northeastern U.S. *Limnol. Oceanogr.*, 42: 1009-1022.
- Bakun, A. and R.H. Parrish. – 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. *ICES J. mar. Sci.*, 48: 343-361.
- Capitanio, F.L., M. Pájaro and G.B. Esnal. – 1997. Appendicularians (Chordata, Tunicata) in the diet of anchovy (*Engraulis anchoita*) in the Argentine Sea. *Sci. Mar.*, 61: 9-15.
- Carreto, J.I. and H.R. Benavides. – 1990. Synopsis on the reproductive biology and early life of *Engraulis anchoita*, and related environmental conditions in Argentine waters. *Phytoplankton. IOC Worksh. Rep. No. 65, Annex V*: 2-5.
- Carreto, J.I., M.L. Lasta, R.M. Negri and H.R. Benavides. – 1981a. Los fenómenos de Marea Roja y toxicidad de moluscos bivalvos en el Mar Argentino. In: V. Angelescu (ed.), *Campañas de investigación pesquera realizadas en el Mar Argentino por los B/I 'Shinkai Maru' y 'Walter Herwig' y B/P 'Marburg'*, años 1978 y 1979. Resultados de la Parte Argentina. *Ser. Contr. Inst. Nac. Invest. Des. Pesq.*, 399, p.181-201.
- Carreto, J.I., R.M. Negri and H.R. Benavides. – 1981b. Fitoplancton, pigmentos y nutrientes. Resultados Campañas III y VI del B/I 'Shinkai Maru', 1978. In: V. Angelescu (ed.), *Campañas de investigación pesquera realizadas en el Mar Argentino por los B/I 'Shinkai Maru' y 'Walter Herwig' y B/P 'Marburg'*, años 1978 y 1979. Resultados de la Parte Argentina. *Ser. Contr. Inst. Nac. Invest. Des. Pesq.*, 399, p.1-101.
- Carreto, J.I., R.M. Negri, H.R. Benavides and R. Akselman. – 1985. Toxic dinoflagellate blooms in the Argentine Sea. In: D.M. Anderson, A.W. White and D.G. Baden (eds.), *Toxic Dinoflagellates*, pp. 147-152. Elsevier, New York.
- Carreto, J.I., H. Benavides, R. Negri and P.D. Glorioso. – 1986. Toxic red-tide in the Argentine Sea. Phytoplankton distribution and survival of the toxic dinoflagellate *Gonyaulax excavata* in a frontal area. *J. Plankton Res.*, 8: 15-28.
- Carreto, J.I., N. G. Montoya, D. Cucchi Colleoni and R. Akselman. – 1998. *Alexandrium tamarense* blooms and shellfish toxicity in the Argentine Sea: A retrospective view. In: B. Reguera, J. Blanco, M.L. Fernández and T. Wyatt (eds.) *Harmful Algae*, pp. 131-134. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO.
- Ciechowski, J.D. and G. Weiss. – 1974a. Distribución de huevos y larvas de merluza, *Merluccius merluccius hubbsi*, en las aguas de la plataforma de la Argentina y Uruguay en relación con la anchoita, *Engraulis anchoita*, y las condiciones ambientales. *Physis A*, 33: 185-198.
- Ciechowski, J.D. and G. Weiss. – 1974b. Estudios sobre la alimentación de larvas de la merluza, *Merluccius merluccius hubbsi* y de la anchoita, *Engraulis anchoita* en el mar. *Physis A*, 33: 199-208.
- Clemmesen, C., R.P. Sánchez and C. Wongtschowski. – 1997. A regional comparison of the nutritional condition of SW Atlantic anchovy larvae, *Engraulis anchoita*, based on RNA/DNA ratios. *Arch. Fish. Mar. Res.*, 45: 17-43.
- Costello, J.H., R. Loftus and R. Wagget. – 1999. Influence of prey detection on capture success for the ctenophore *Mnemiopsis leidyi* feeding upon adult *Acartia tonsa* and *Oithona colcarva* copepods. *Mar. Ecol. Prog. Ser.*, 191: 207-216.
- Cushing, D. – 1989. A difference in structure between ecosystems in strongly stratified waters and those that are only weakly stratified. *J. Plankton Res.*, 11: 1-13.
- Daan, N., P.J. Bromley, J.G.R. Hislop and N.A. Nielsen. – 1990. Ecology of the North Sea. *Neth. J. Sea Res.*, 26: 342-386.

- Daan, R. – 1987. Impact of egg predation by *Noctiluca miliaris* on the summer development of copepod populations in the southern North Sea. *Mar. Ecol. Prog. Ser.*, 37: 9-17.
- Ehrlich, M.D. and J.D. Ciechowski. – 1994. Reseña sobre la distribución de huevos y larvas de merluza (*Merluccius hubbsi*) basada en veinte años de investigaciones. *Frente Marítimo*, 15 A: 37-50.
- Ehrlich, M.D. – 1998. *Los primeros estadios de vida de la merluza Merluccius hubbsi Marini 1933, como aporte al conocimiento de su reclutamiento y estructura poblacional*. Tesis presentada para optar al título de Doctor en Ciencias Biológicas, Universidad de Buenos Aires, 318 pp.
- Esnal, G.B. – 1981. Thaliacea: Salpidae and Appendicularia. In: D. Boltovskoy (ed.) *Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con zooplancton marino*, pp. 793-827. Inst. Nac. Inv. Des. Pesq., Mar del Plata.
- Franz, H.G. and S.R. Gonzalez. – 1995. The production of *Oithona similis* (Copepoda: Cyclopoida) in the Southern Ocean. *ICES J. mar. Sci.*, 52: 549-555.
- Glorioso, P.D. – 1987. Temperature distribution related to shelf-sea fronts on the Patagonian Shelf. *Cont. Shelf Res.*, 7: 27-34.
- Glorioso, P.D. – 2000. Patagonian shelf 3D tide and surge model. *J. Mar. Syst.*, 24: 141-151.
- Glorioso, P.D. and J.H. Simpson. – 1994. Numerical modelling of the M2 tide on the northern Patagonian Shelf. *Cont. Shelf Res.*, 14: 267-278.
- Glorioso, P.D. and R.A. Flather. – 1995. A barotropic model of the currents off SE South America. *J. Geophysical Res.*, 100: 13427-13440.
- Glorioso, P.D. and R.A. Flather. – 1997. The Patagonian Shelf tides. *Prog. Oceanogr.*, 40: 263-283.
- Guerrero, R.A. and A.R. Piola. – 1997. Masas de agua en la plataforma continental. In: E.E. Boschi (ed.), *El Mar Argentino y sus recursos pesqueros. Tomo 1. Antecedentes históricos de las exploraciones en el mar y las características ambientales*, pp. 107-118 Inst. Nac. Inv. Des. Pesq., Mar del Plata.
- Hansen, J.E., P. Martos and A. Madirolas. – 2001. Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring-early summer. *Fish. Oceanogr.*, 10: 193-206.
- Holligan, P.M., R.R. Harris, R.C. Newell, A. Harbour, R.N. Head, E.A.S. Linley, M.I. Lucas, P.R.G. Tranter and C.M. Weekley. – 1984. Vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel. *Mar. Ecol. Prog. Ser.*, 14: 111-127.
- Kjørboe, T. – 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Adv. Mar. Biol.*, 29: 1-72.
- Kjørboe, T. and K. Johansen. – 1986. Studies of larval herring (*Clupea harengus* L.) patch in the Buchan area. IV. Zooplankton distribution and productivity in relation to hydrographic features. *Dana*, 6: 37-51.
- Kjørboe, T. and J. Titelman. – 1998. Feeding, prey selection and prey encounter mechanisms in the heterotrophic dinoflagellate *Noctiluca scintillans*. *J. Plankton Res.*, 20: 1615-1636.
- Kjørboe, T., P. Munk, K. Richardson, V. Christensen and H. Paulsen. – 1988. Plankton dynamics and larval herring growth, drift and survival in a frontal area. *Mar. Ecol. Prog. Ser.*, 44: 205-219.
- Le Févre, J. – 1986. Aspects of the biology of frontal systems. *Adv. Mar. Biol.*, 23: 163-299.
- Le Févre, J. and J.R. Grall. – 1970. On the relationship of *Noctiluca* swarming off the western coast of Brittany with hydrological features and plankton characteristics of the environment. *J. Exp. Mar. Biol. Ecol.*, 4: 287-306.
- Lopes, R.M., F.P. Brandini and S.A. Gaeta. – 1999. Distribution patterns of epipelagic copepods off Rio de Janeiro (SE Brazil) in summer 1991/1992 and winter 1992. *Hydrobiologia*, 411: 161-174.
- Martos, P. – 2000. Características del campo térmico en la plataforma patagónica entre 42° y 45°S. *Inf. Téc. Int. Inst. Nac. Inv. Des. Pesq.*, 27, 13 pp.
- Martos, P. and R. Sánchez. – 1997. Caracterización oceanográfica de regiones frontales en la plataforma patagónica en relación con áreas de desove y cría de la anchoíta (*Engraulis anchoita*). *10° Coloquio Argentino de Oceanografía*, 4-5 Septiembre 1997, IADO-CONICET, Bahía Blanca. POSTER.
- Mianzan, H.W. and R.A. Guerrero. – 2000. Environmental patterns and biomass distribution of gelatinous macrozooplankton. Three study cases in the South-western Atlantic Ocean. *Sci. Mar.*, 64(Sup. 1): 215-224.
- Mölemkamp, M. – 1996. *Untersuchungen zur kleinskaligen Verteilung von Mikro- und Mesozooplankton im oberen Pelagial des südamerikanischen Schelfmeeres unter Erprobung eines neuen automatischen Messgerätes*. Ph.D. Thesis, Hamburg University, 112 pp.
- Munk P, P.O. Larsson, D.S. Danielssen and E. Moksness. – 1999. Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea. *Mar. Ecol. Prog. Ser.*, 177: 221-233
- Nakamura, Y. and J. Turner. – 1997. Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? *J. Plankton Res.*, 19: 1275-1288.
- Negri, R.M. – 1994. Material particulado y fitoplancton en tres secciones en la plataforma continental de Uruguay y Argentina. *11° Simposio Científico Tecnológico Comisión Técnica Mixta del Frente Marítimo*. Mar del Plata, 5-8 Diciembre 1994. POSTER.
- Nielsen, T.G. and M. Sabatini. – 1996. Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. *Mar. Ecol. Prog. Ser.*, 139: 79-93.
- Nielsen, T.G. and P. Munk. – 1998. Zooplankton diversity and the predatory impact by larval and small juvenile fish at the Fisher Banks in the North Sea. *J. Plankton Res.*, 20: 2313-2332.
- Nielsen, T.G., B. Løkkegaard, K. Richardson., F.B. Pedersen and L. Hansen. – 1993. Structure of plankton communities in the Dogger Bank area (North Sea) during a stratified situation. *Mar. Ecol. Prog. Ser.*, 95: 115-131.
- Orensanz, J.M., M. Pascual and M. Fernández. – 1991. Chapter 14: Fisheries and Aquaculture, Argentina. In: S.E. Shumway (ed.), *Developments in Aquaculture and Fisheries Science 21, Scallops: biology, ecology and aquaculture*, pp. 981-999. Elsevier, Amsterdam.
- Pájaro, M. – 1989. *Factor de condición y condición nutricional en larvas y postlarvas de anchoíta en diferentes áreas de cría del Mar Argentino*. Seminario de Licenciatura, Univ. Nac. Mar del Plata, 61 pp.
- Pingree, R.D., P.M. Holligan and G.T. Mardell. – 1978. The effects of vertical stability on phytoplankton distributions in the summer on the northwest European Shelf. *Deep Sea Res.*, 25: 1011-1028.
- Pitcher, G.C., A.J. Boyd, D.A. Horstman and B.A. Mitchell-Innes. – 1998. Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. *Mar. Ecol. Prog. Ser.*, 172: 253-264.
- Podestá, G.P. – 1989. Migratory pattern of Argentine hake *Merluccius hubbsi* and oceanic processes in the Southwestern Atlantic Ocean. *Fish. Bull.*, 88, 167- 177.
- Ramírez, F.C. – 1981. Zooplankton y producción secundaria. Parte I. Distribución y variación estacional de los copépodos. In: V. Angelescu (ed.) *Campañas de investigación pesquera realizadas en el Mar Argentino por los B/I 'Shinkai Maru' y 'Water Herwig' y B/P 'Marbug', años 1978 y 1979. Resultados de la Parte Argentina*. *Ser. Contr. Inst. Nac. Inv. Des. Pesq.*, 383, p. 202-212.
- Ramírez, F.C. and T. Björnberg. – 1981. Distribución horizontal, por masas de agua, de los copépodos más frecuentes y abundantes (indicadores biológicos) en el Atlántico Sudoccidental. In: D. Boltovskoy (ed.), *Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con zooplancton marino*, p. 595. *Inst. Nac. Inv. Des. Pesq.*, Mar del Plata.
- Ramírez, F.C. and G.M. Pérez Seijas. – 1985. New data on the ecological distribution of cladocerans and first local observations on reproduction of *Evadne normanni* and *Podon intermedius* (Crustacea, Cladocera) in Argentine Sea waters. *Physis A*, 43: 131-143.
- Richardson, K., T.G. Nielsen, F.B. Pedersen, J.P. Heilmann, B. Løkkegaard and H. Kaas. – 1998. Spatial heterogeneity in the structure of the planktonic food web in the North Sea. *Mar. Ecol. Prog. Ser.*, 168: 197-211.
- Rivas, A.L. – 1997. Current-meter observations in the Argentine Continental Shelf. *Cont. Shelf Res.*, 17: 391-406.
- Sánchez, R.P. and J.D. Ciechowski. – 1995. Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. *Sci. Mar.*, 59: 455-478.
- Sánchez, R.P., J. Alheit, P. Martos and M. Pájaro. – 1998. The spawning and early life of *Engraulis anchoita* in the tidal front

- off Patagonia. *ICES Annual Meeting*, Cascais, Portugal, 16-19 September, ICES C.M. 1998/R:1.
- Santos, B.A. – 1993. Zooplankton as potential food in the spawning ground of Patagonian anchovy and hake. *Fifth IOC Workshop on Sardine/Anchovy recruitment project (SARP) in Southwest Atlantic*, Buenos Aires, Argentina, 18-21 December 1993.
- Santos, B.A. and F.C. Ramírez. – 1995. Distribución y abundancia de copépodos en el sistema frontal de Península Valdés, durante florecimientos fitoplanctónicos. *Thalassas*, 11: 133-142.
- Servicio Meteorológico Nacional. – 1985. Estadística Climatológica, 1961-1970, n° 35. Fuerza Aérea Argentina, Buenos Aires, Argentina, 188 pp.
- Servicio Meteorológico Nacional. – 2000. Cien Años de Trelew con el Tiempo. Fuerza Aérea Argentina, Dpto. Climatología, Buenos Aires, Argentina, 33 pp.
- Sherman, K., M. Grosslein, D. Mountain, D. Busch, J. O'Reilly and R. Theroux. – 1988. The continental shelf ecosystem off the Northeast coast of the United States. In: H. Postuma and J.J. Zijlstra (eds.), *Ecosystems of the world 27: Continental shelves*, pp. 279-337. Elsevier, Amsterdam.
- Simpson, J.H. – 1981. The shelf-sea fronts: implications of their existence and behaviour. *Phil. Trans. Royal Soc. London*, 302 A: 531-546.
- Sullivan, B.K. and D. Van Keuren. – 2001. Zooplankton response to spring invasion of Narragansett Bay by the ctenophore *Mnemiopsis leidyi*. Abstract *ASLO Aquatic Sciences Meeting*, February 12-16, 2001, Albuquerque, New Mexico.
- Sullivan, B.K., D. Van Keuren and M. Clancy. – 2001. Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. *Hydrobiologia*, 451: 113-120.
- Viñas, M.D. and F.C. Ramírez. – 1995. Gut analysis of first feeding anchovy larvae from Patagonian spawning areas in relation to food availability. *Arch. Fish. Mar. Res.*, 43: 231-256.
- Viñas, M.D. and B.A. Santos. – 2000. First-feeding of hake (*Merluccius hubbsi*) larvae and prey availability in the North Patagonian spawning area. Comparison with anchovy. *Arch. Fish. Mar. Res.*, 48: 242-254.
- Viñas, M.D., F.C. Ramírez, B.A. Santos and G.M. Pérez Seijas. – 1992. Zooplankton distribuido en el área de desove y de crianza norpatagónica de la merluza (*Merluccius hubbsi*). *Frente Marítimo*, 11 A: 105-13.
- Waggett, R. and J.H. Costello. – 1999. Capture mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, preying on the copepod *Acartia tonsa*. *J. Plankton Res.*, 22: 2037-2052.
- Walker, D.R. and W.T. Peterson. – 1991. Relationships between hydrography, phytoplankton production, biomass, cell size and species composition, and copepod production in the Southern Benguela upwelling system in April 1988. *S. Afr. J. mar. Sci.*, 11: 289-305.
- Scient. ed.: A. Ianora