Seasonal pattern of zooplankton biomass in the Argentinian shelf off Southern Patagonia (45°-55°S)*

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SUMMARY: Zooplankton biomass in the Argentine Sea off Southern Patagonia was measured during thirteen research cruises carried out between 1992 and 1997 and interpreted in the context of the feeding habits of regional fish resources. Samples were collected with a Nackthai sampler (400-500 μm mesh size) towed obliquely through the water column. Wet weights of the size fraction smaller than 5 mm (mostly made up of copepods), amphipods, euphausiids, mysids and chaetognaths were determined separately. Total zooplankton biomass increased from spring to summer or early autumn. The highest values were consistently located in coastal waters between 51° and 52°S and near the shelf-break from 46° to 48°S. In spring most of the biomass of the entire region was built up of copepods. During late summer-early autumn the contribution of the larger groups increased, with amphipods dominating in the coastal area and euphausiids being more abundant in deeper waters. Mysid biomass was significant only in the innermost coastal area in spring and autumn. The occurrence and densities of chaetognaths increased offshore.

Key words: zooplankton, biomass, copepods, amphipods, euphausiids, chaetognaths, Argentine Sea, Patagonia.

INTRODUCTION

Zooplankton play a key role in pelagic food chains by linking primary producers and secondary consumers. As food for larval and planktivorous fish, zooplankton availability is considered to be one of the main factors determining year class strength of commercial species (Cushing, 1984; Kiørboe, 1991, 1993). There is increasing evidence that depletion of demersal or midwater top predators, mainly as a consequence of intensive fishing, has resulted in an increased biomass of small zooplanktivorous pelagic fish (e.g. Ivanov and Beverton, 1985; Parsons, 1993; Parrish, 1995). High concentrations of zooplankton food stock may in turn fuel these increases and allow some small pelagics to reach larger population sizes (e.g. Kane, 1993).

The first contributions to the current knowledge on zooplankton of Austral Patagonia derived from the classic expeditions during the 18th, 19th and early 20th centuries as reviewed by Ehrlich and Sánchez (1990) and Angelescu and Sánchez (1995). Being on the way to Antarctica, this region has been frequently visited by international expeditions from which some occasional references have emerged. They – and also some more recent Argentinian works – mostly refer to taxonomy and geographical-ecological distributions of major

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groups (e.g. Boltovskoy, 1981, 1999). In the late 1970's the basic hydrography and plankton of the entire Argentine Sea from 35° to 55°S were studied throughout an annual cycle by the 'Walter Herwig' and 'Sinkai Maru' surveys. Hence, though the study focused mainly on the northern region down to 46°S, the production cycle was outlined for the first time (Carreto *et al.*,1981b) and the pattern of zooplankton biomass was related to the abundance of fish eggs and larvae (Ciechomski and Sánchez, 1983). From the same collections, the extensive distribution – including southern Patagonia – of the dominant copepod species (Ramírez, 1981), hyperiid amphipods (Ramírez and Viñas, 1985), chaetognaths (Mazzoni, 1983, 1988) and pteropods (Dadon, 1986, 1990, 1992) were also reported on in detail, as well as the seasonal changes in the populations of the dominant species of euphausiids (Ramírez and Dato, 1983). Post 1970s information was limited to biomass estimates conducted during two cruises on the Patagonian shelf (Fernández Aráoz and Viñas, 1994; Santos, 1994) and to the macrozooplankton biomass and assemblages found around the Malvinas Islands (Rodhouse *et al.*, 1992; Tarling *et al.*, 1995).

The continental shelf and adjacent waters off Southern Patagonia (Fig. 1) constitute one of the main fishing grounds of the Argentine Sea. Several major resources occur in the region, such as longtail hake, southern blue whiting, Argentinian common hake, austral hake, Patagonian toothfish, austral cod, kinglip and squid (Otero *et al.*, 1981; Brunetti and Pérez Comas, 1989; Bezzi and Dato, 1995; Madirolas *et al.,* 1997; Wöhler *et al.,* 1999; Wöhler and Marí, 1999). Patagonian sprat is also distributed in the area (Sánchez *et al.*, 1995; Sánchez *et al.*, 1997). This is a key zooplanktivorous fish as it is a main food item for many of the above species and consequently constitutes a strong link between trophic levels (Angelescu *et al.*, M.S.). The exploitation of austral species began in the late 1970's. From then on, a progressive decrease in the biomass of most commercial fish has been noticed (Bertolotti *et al.*, 1996).

From 1992 onwards, regular Argentinian fisheries assessment surveys have been carried out in Austral Patagonia (Wöhler *et al.,* 1999). Though they covered diverse sub-areas and seasons depending on the target fish species, sampling during these cruises yielded a unique zooplankton data set. This provided the opportunity to assemble the most intensive up-to-date spatial coverage for the region. The purpose of this paper is to describe the overall pattern of zooplankton biomass occurring in southern Patagonia by compiling the most recent data. This information establishes a baseline for food stock of planktivorous fish within a region that appears to be a main feeding ground of several commercial species, which are under increasing fishing pressure.

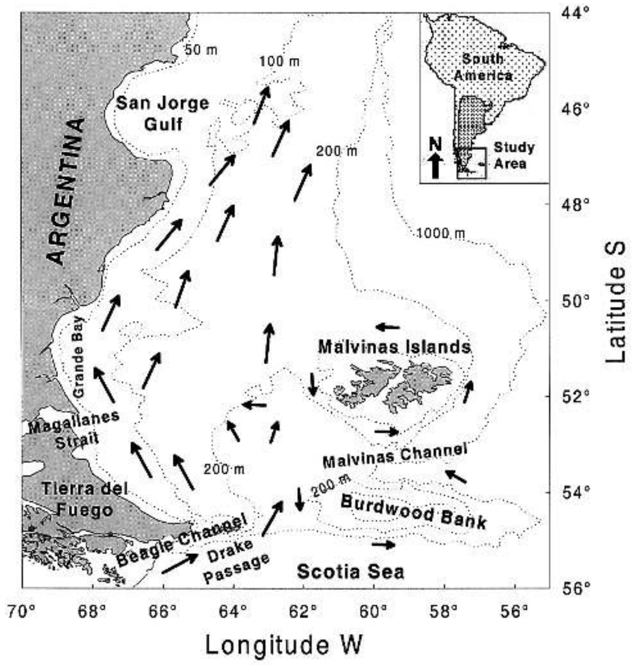

FIG. 1. – General major circulation and landmarks of the Argentine Sea off southern Patagonia. Modified from Piola and Rivas (1997).

THE STUDY AREA

The study area extended mostly over the Argentinian continental shelf and also, on some occasions, the deeper waters located to the SW of the Malvinas Islands and the Burdwood Bank. A main feature of the continental shelf is the shallow depth gradient as compared to the adjacent steep continental slope (Parker *et al.,* 1997). Within the shelf there are two subareas: a 100 km coastal band where the depth increases sharply down to 100 m, and an outer wide plain 250-450 km in width with a more gradual slope. At the latitude of the Malvinas Islands, the shelf reaches its maximum width of 850 km (Guerrero *et al.,* 1999).

Waters over most of the Austral Patagonia shelf are of subantarctic origin, and are produced by mixing of the cool, nutrient-rich waters of the Malvinas Current with coastal waters highly diluted by run-off from the Magellanes Strait and the Beagle Channel. Three water masses can be identified by their salinities: Malvinas, Coastal and Shelf waters (Bianchi *et al.,* 1982). The general water circulation on the Argentinian shelf has recently been reviewed by Piola and Rivas (1997).

The occurrence of fronts of different kinds is another main characteristic of the southern Patagonia region (Guerrero and Piola, 1997). Shelf-sea tidal and convergence fronts have been identified along the coast between 50° S and De los Estados Island in summer, and around the Malvinas Islands and near the Burdwood Bank in late winter (Sánchez *et al.*, 1995; Sánchez *et al.,* 1997; Wöhler *et al.*, 1999; Guerrero *et al.,*1999; Reta, M.S.). Another front extending along the shelf-break all year long, although less developed in winter, is created by the encounter of shelf waters with the Malvinas Current (Carreto *et al.*, 1995; Bertolotti *et al.*, 1996).

The general major circulation and landmarks of the Argentine Sea off southern Patagonia are shown in Figure 1. For general descriptive purposes, we have herein considered three geographic areas according to bottom depth: the Inner-Coastal Area (< 50 m), the Outer-Coastal Area (50 - 100 m) and the Mid-Outer shelf Area (>100 m).

MATERIAL AND METHODS

Field data were collected during the thirteen surveys shown in Table 1. Zooplankton samples (N = 563) were collected with a Nackthai sampler (20 cm mouth diameter, 2.5 m net length, 400-500 μm mesh size) towed obliquely through the water column from near the bottom to the surface, or from a maximum depth of 500 m at deeper stations. Sampling was normally conducted at dusk, dawn or night time in view of the general pattern of aggregation and vertical migration of the dominant groups. Depth and towing speed (*ca*. 3 knots) were monitored by means of a depth sensor. A General Oceanic mechanical flowmeter was used to estimate the water volume filtered (normally 20-100 m^3). The size of the animals collected ranged mostly between 0.4 mm and *ca*. 25 mm. It follows that the fraction actually sampled was built up by large mesozooplankton and small macrozooplankton, and thus food of first-feeding fish larvae was ruled out. Abundance of adult euphausiids and amphipods may still have been underestimated due to the small mouth of the gear.

Wet weights were either determined on board immediately after collection, or the samples were preserved in 5% buffered formalin for subsequent analysis in the laboratory. Zooplankton (usually subsamples) were sorted into two size fractions (larger and smaller than 5 mm) by individually picking late juveniles and adults of euphausiids/mysids, amphipods and chaetognaths. The remaining smaller fraction was drained through a preweighed 200 μm mesh filter before biomass determination. Each fraction as well as the sorted groups (euphausiids, hyperiid amphipods and chaetognaths) were weighed separately using a small manual scale (± 0.2 g) after removing as much water as possible. Total zooplankton biomass was estimated from the sum of the two size fractions. Gelatinous zooplankton was not common in the samples. When they were present, and always in low numbers, their wet weights were disproportionally too high to be comparable to the major groups. Salps, siphonophors, jellyfish and doliolids were therefore excluded from the analysis.

TABLE 1. – Cruises carried out in the southern Argentinian shelf (45°-55°S) which provided the present zooplankton data set.

Season	Date	Sub-area	Position	Cruise	R.V.
Winter	22 Jul-16 Aug 93	Mid - Outer Shelf	48° - 55° S	OB-08/93	Cap. Oca Balda
Late Winter	11-30 Sep 94	Outer Shelf	47° - 55° S	OB-07/94	Cap. Oca Balda
Late Winter	04-25 Sep 95	Outer Shelf	52° - 55° S	OB-10/95	Cap. Oca Balda
Late Winter	16-28 Sep 96	Outer-Shelf	52° - 55° S	OB-11/96	Cap. Oca Balda
Spring	07-22 Nov 92	Mid - Outer Shelf	46° - 52° S	EH-09/92 (*)	Dr. E. Holmberg
Spring	31 Oct-25 Nov 94	Mid - Outer Shelf	47° - 55° S	OB-09/94	Cap. Oca Balda
Spring	23 Nov-06 Dec 96	Coastal	50° - 55° S	OB-13/96	Cap. Oca Balda
Summer	07 Jan-02 Feb 93	Mid - Outer Shelf	45° - 51° S	EH-01/93 (**)	Dr. E. Holmberg
Summer	04-21 Feb 95	Mid - Outer Shelf	45° - 51° S	OB-03/95	Cap. Oca Balda
Summer	07-24 Mar 95	Mid - Outer Shelf	51° - 55° S	OB-04/95	Cap. Oca Balda
Late Summer	15 Mar-04 Apr 97	Mid - Outer Shelf	47° - 53° S	OB-04/97	Cap. Oca Balda
Autumn	21 Mar-09 May 94	Mid - Outer Shelf	49° - 55° S	OB-04/94	Cap. Oca Balda
Autumn	19 Apr-01 May 96	Coastal	50° - 55° S	EH-04/96	Dr. E. Holmberg

(*) from Fernández Aráoz and Viñas (1994); (**) from Santos (1994)

RESULTS

Overall pattern of total zooplankton biomass

The distribution of total zooplankton biomass in each season is shown in Figure 2. The lowest zooplankton concentrations were recorded in winter when values hardly above 100 mg WW.m^{-3} occurred in the entire region. By late spring (November) biomass on average increased threefold from its winter low. The highest values at that time ranged from 1000 to 1500 mg WW m^{-3} and were located in the middle shelf in the northern area (47°-50°S) and in the inner coastal waters in the southern area (50°-55°S). The highest biomass concentrations were recorded in late summer (February-March), when densities ranging from 2000 to 3000 mg WW m^{-3} occurred in the coastal area of the southern region somewhat beyond the 100 m isobath. Values decreased to 100-500 mg WW.m^{-3} in middle and outer shelf waters. On the other

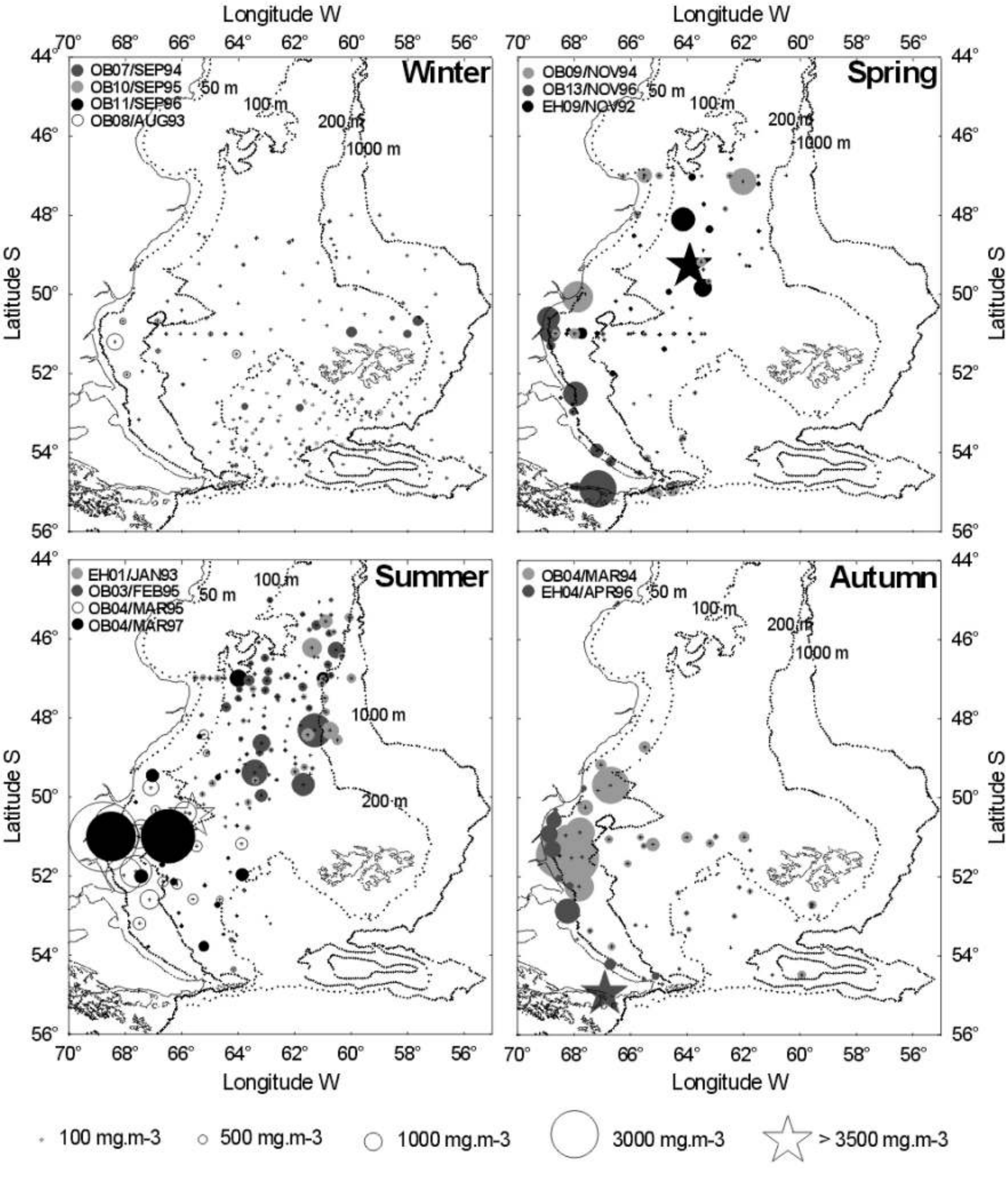

FIG. 2. – Seasonal synoptic distribution of total zooplankton biomass (mg WW m^{-3}) in Argentinian waters off southern Patagonia recorded during the several surveys listed in Table 1.

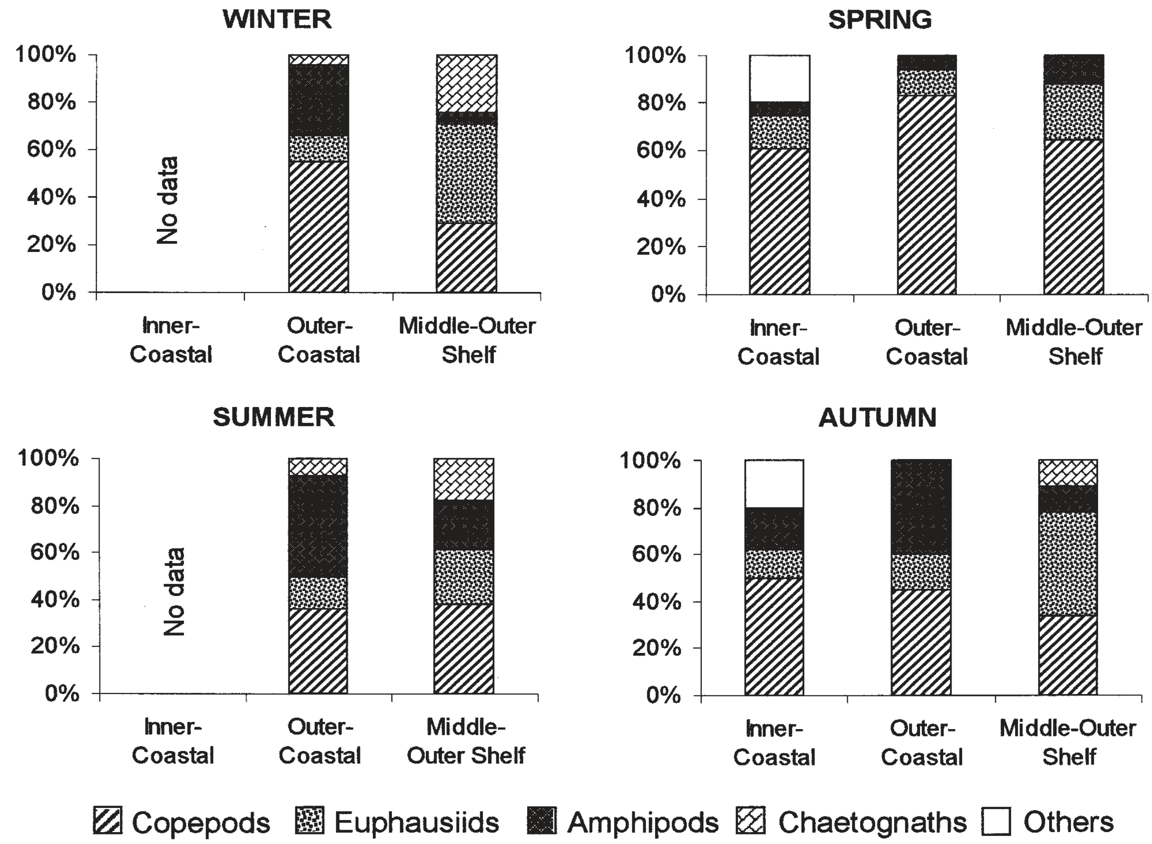

FIG. 3. – Seasonal relative biomass of major taxa of zooplankton in inner coastal (<50 m depth), outer coastal (>50-100 m depth) and middle outer shelf (>100 m depth) waters off Austral Patagonia. Averaged values of the cruises carried out in 1992-1997. Chaetognaths were not absent in spring but data are lacking for that season.

hand, in the northern area the highest summer values were located in outer coastal and outer shelf waters. In early autumn densities remained high in the southern coastal area (< 100 m depth) but decreased in middle shelf waters.

Zooplankton biomass increased from spring time until summer. These high summer biomass values extended to early autumn south of 49°S. The bulk of biomass in late summer/early autumn was consistently located in coastal waters less than *ca*. 100 m deep between 51° and 52°S (Grande Bay). High values were also regularly found near the shelf-break from *ca*. 46° to 48°S in summer, but no data were available to show whether autumn shelf break concentrations remained high or decreased.

Size-fractionated biomass and relative major taxa composition

The <5 mm size fraction consisted most frequently of copepods, though occasionally ostracods, pteropods, juvenile euphausiids and amphipods, other crustacean larvae or fish eggs were also present. Nevertheless, it can be considered as portraying main trends of Copepoda biomass. The biomass dominating groups in the >5 mm fraction were euphausiids and amphipods (Fig. 3). The low winter biomasses were dominated in the outer-coastal area by the smaller fraction. In middle and outer shelf waters, the >5 mm fraction accounted on average for 70 % of total zooplankton biomass with euphausiids as dominants (42%) and chaetognaths as important contributors (24%). In spring 60-80% of the biomass of the whole region was made up of copepods. In the inner-coastal area decapod larvae and mysids were also important at that time in the small and large size fractions respectively. It has to be noted that chaetognaths were not totally absent but separate weight data are lacking for that season. Throughout late summer and early autumn copepods still accounted on average for about 40% of total biomass, but the relative importance of the larger fraction increased. It was mostly made up of hyperiid amphypods in the coastal area (47%), decreasing to the further deeper waters where euphausiids become more abun-

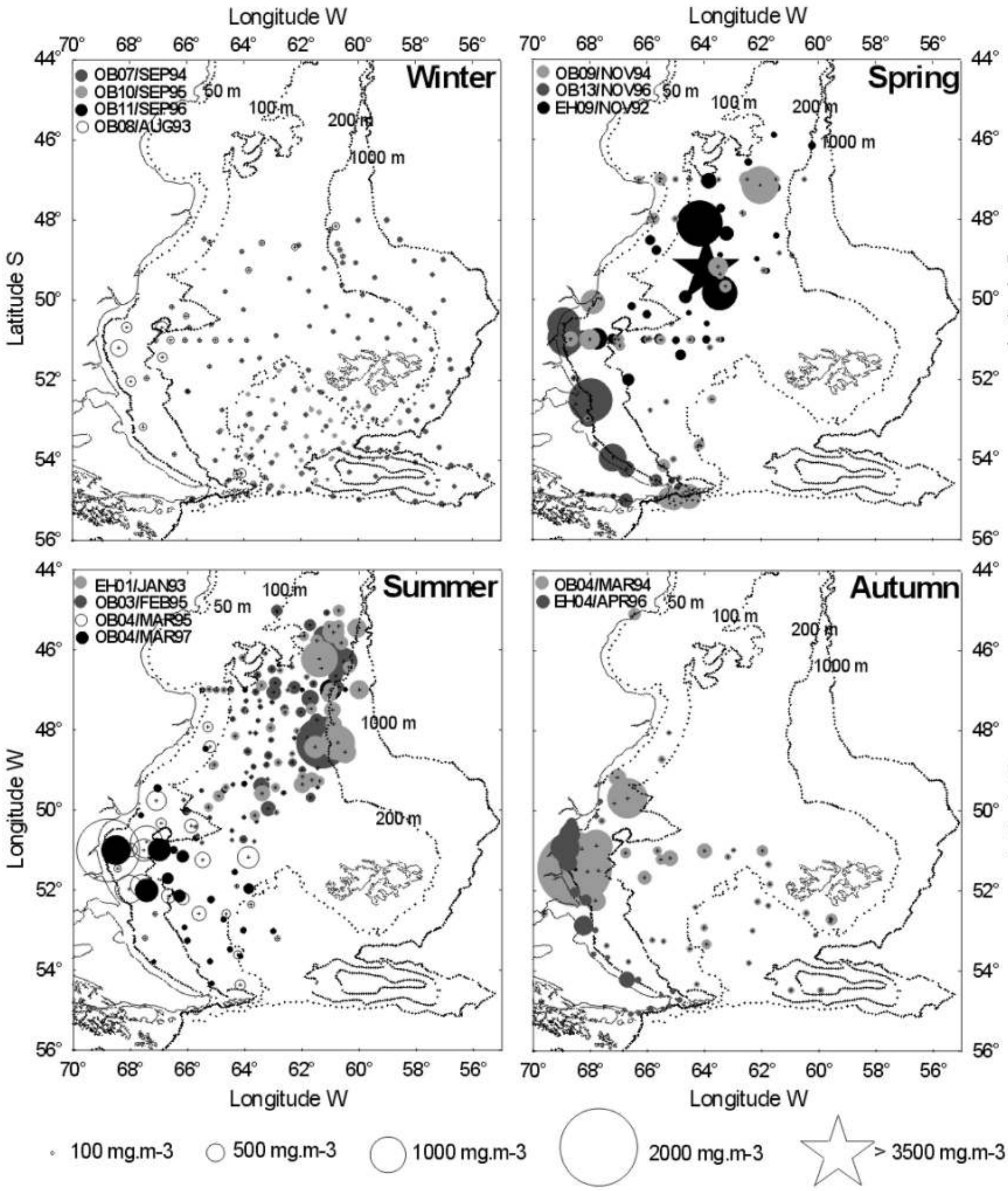

FIG. 4. – Seasonal synoptic distribution of the <5 mm size fraction (= Copepoda) biomass in southern Patagonia. Cruise references shown in Table 1.

dant, particularly in autumn (44%). In this season mysids prevailed again in the >5 mm fraction of the inner coastal area.

Major taxa distribution

Smaller size fraction - Copepoda (Fig. 4). Copepods were spread over the entire region, showing high biomass concentrations for most seasons. In spring they peaked in middle shelf waters of the northern area, while to the south the highest values occurred in inner coastal waters. In summer the highest concentrations were recorded offshore near the shelf-break in the northern area down to about 49°S and in outer coastal waters southwards. Autumn data are limited to the southern area where copepod biomass reached its annual maximum in the coastal subarea between 50° and 52°S.

Euphausiacea (Fig. 5). The biomass of euphausiids was generally low in the entire region during most of the annual cycle. Relatively higher

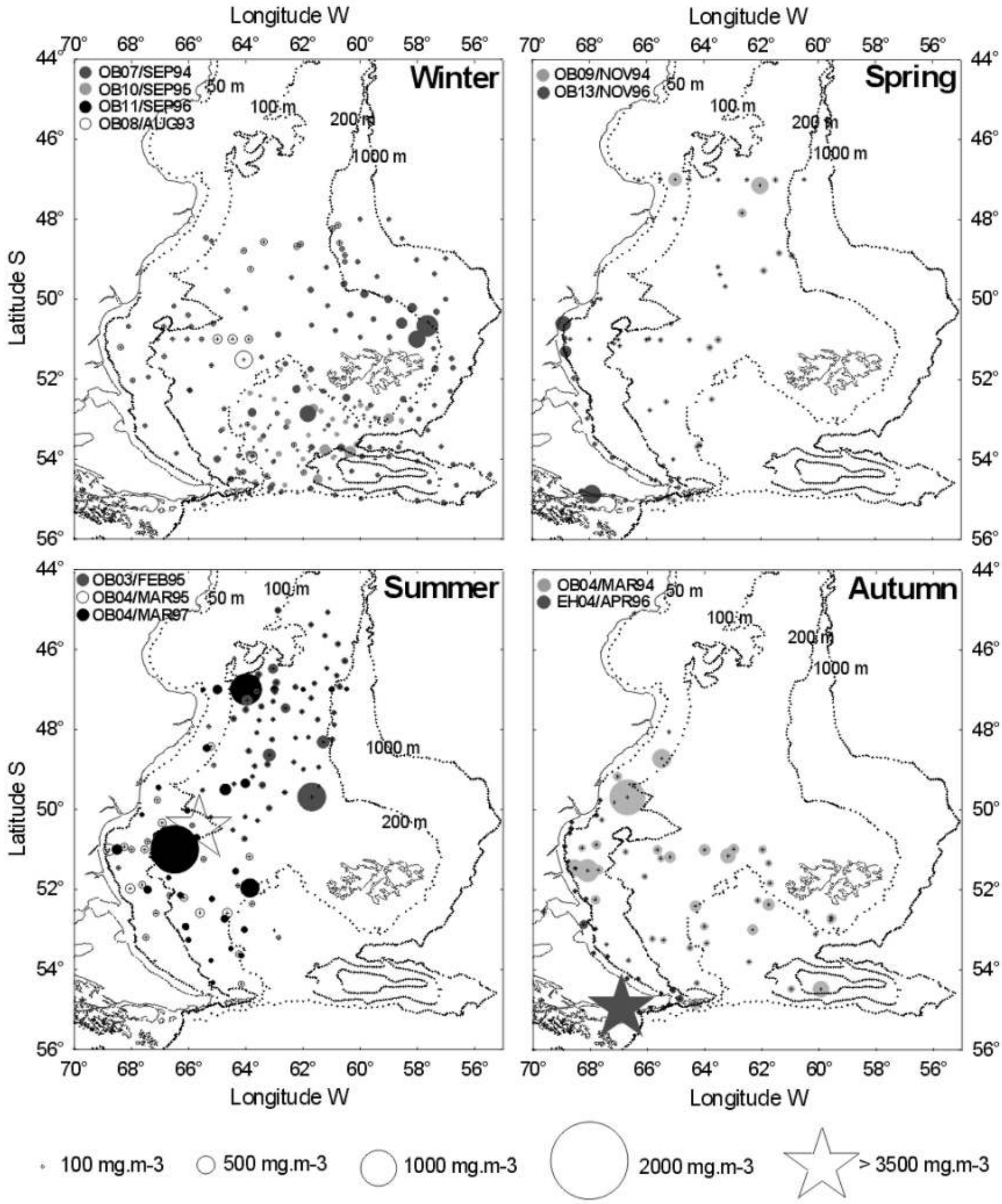

FIG. 5. – Seasonal synoptic distribution of Euphausyda biomass in southern Patagonia. Cruise references shown in Table 1.

values were recorded in the neighborhood of the Malvinas Islands in winter, while in summer and autumn high concentrations occasionally occurred in mid-outer shelf waters and near the coast respectively.

Amphipoda (Fig. 6). During winter and spring, the biomass of hyperiid amphipods was low and uniformly distributed in the whole region. It peaked noticeably in summer and autumn in coastal waters between 50° and 52°S. A secondary peak of biomass occurred in middle shelf waters of the northern area in summer. This group was nearly monospecific throughout all seasons and years, being almost exclusively built up of *Themistho gaudichaudii*.

Chaetognatha were usually abundant in numbers but contributed little in terms of absolute biomass. They normally occurred from outer-coastal waters to deeper areas, their presence and abundance increasing offshore.

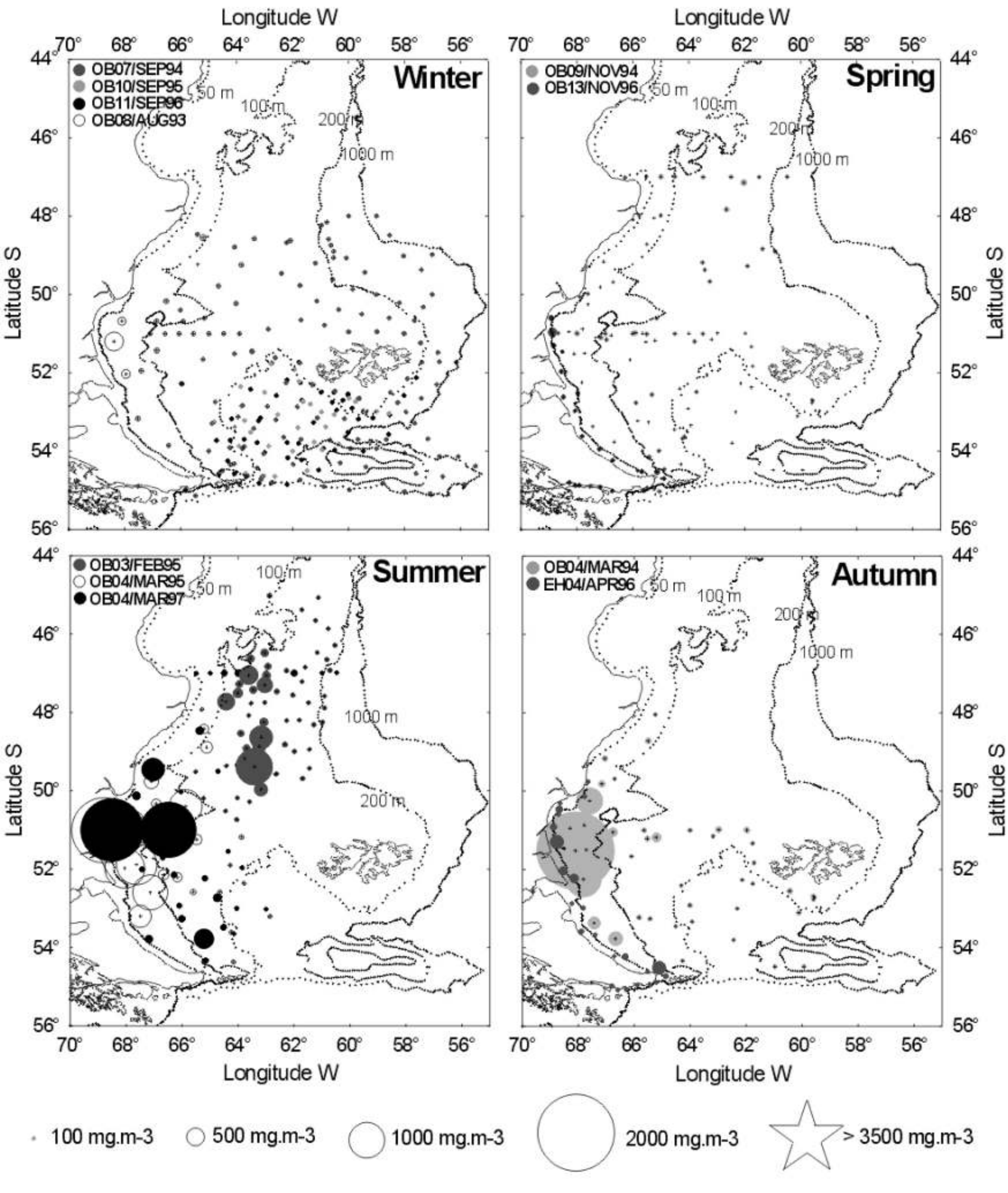

FIG. 6. – Seasonal synoptic distribution of Amphipoda biomass in southern Patagonia. Cruise references shown in Table 1.

DISCUSSION

This is so far the largest gathering of information on zooplankton biomass reported for the southern Patagonian region. We are aware of the methodological constraints introduced as the seasonal data set was not provided by a single sampling programme with a proper space-time coverage. Instead, it was gathered from several cruises carried out in different years. This is likely to have introduced an unknown amount of bias but will not have modified the main seasonal trends. Furthermore, the patterns found in the various surveys conducted during a same season and area were quite consistent in different years.

Present knowledge on the overall patterns of plankton biomass occurring in the Argentine Sea from 35° to 55°S comes from the pioneering studies by Carreto *et al.* (1981a, 1981b) and Ciechomski and Sánchez (1983). In the northern region down to 46°S, the plankton production cycle follows the typical development and breakdown of the seasonal thermocline characteristic of cold-temperate seas, the main phytoplankton peak occurring in spring and the secondary one in autumn. Zooplankton biomass peaks following phytoplankton blooms. In contrast, the autumn phytoplankton pulse does not occur at the higher austral latitudes, probably due to light limitation (Bakun and Parrish, 1991), but a single longer phytoplankton maximum develops during late spring and summer (Angelescu and Prenski, 1987). Accordingly, we found that zooplankton biomass peaks during late summer and early autumn following the annual phytoplankton maximum. This was a regular fact throughout the cruises analysed. Ciechomski and Sánchez (1983) also reported maxima zooplankton biomass in summer for the southern region. The high values we found in autumn are, however, mentioned for the first time. The differences can be attributed to the more intensive spatial coverage of the present data set.

At least two relatively richer areas can be distinguished during summertime in the Austral Patagonia region: (1) coastal waters between 51° and 52°S (Grande Bay) and (2) offshore waters between 46° and 48°S. These seasonally-enhanced feeding environments may constitute potential nursery grounds for the fish species distributed in the region. The southern coastal area has highly complex hydrography and circulation patterns. A main feature is the occurrence in summer and early autumn of frontal systems created by tidal mixing and/or convergence of different water types as reported by Sánchez *et al.*(1995, 1997), Wöhler *et al. (*1999) and Reta (M.S.). The dynamics of these fronts, which at present are poorly known, may have a great effect on either the production or the concentration of plankton, and thus lead to the high densities of zooplankton biomass that we recorded in the area during these seasons. On the other hand, the local plankton production in the offshore area located between 46° and 48°S appears to be related to a shelf-break front (Carreto *et al*., 1995; Bertolotti *et al.,* 1996).

Major zooplankton groups reported on in this study have been repeatedly quoted as food resources for the fish species occurring in the region. The hyperiid amphipod *Themistho gaudichaudii* and the euphausiid *Euphausia lucens* are the main food items of longtail hake in summer (Wöhler e*t al*., 1999; Sánchez, 1999; Álvarez Colombo *et al.,* M.S.); euphausiids prevail in the diet of juveniles and adults of southern blue whiting all year long while copepods and hyperiid amphipods have a more seasonal importance (Otero, 1976, 1977; Perrotta, 1982); calanoid copepods, euphausiids, hyperiid amphipods and mysids are main food sources for common hake (Angelescu and Prenski, 1987); squid, even large-sized ones, feed extensively on *T. gaudichaudii* during summer-autumn in Patagonian shelf waters (Ivanovic and Brunetti, 1994); all development stages of copepods, mysids and secondarily euphausiids are the dominat items in the diet of Patagonian sprat (Ramírez, 1976; Angelescu *et al*., M.S.).

It is apparent from the above that the hyperiid amphipod *Themisto gaudichaudii* is a crucial food item for many of the fish species distributed in the region and thus, along with the Patagonian sprat, it is another key species in the trophic dynamics of Austral Patagonia. The species occurs widely all over the continental shelf and normally outnumbers any other (Ramírez and Viñas, 1985; Álvarez Colombo and Viñas, 1994). In accordance with our findings, dense aggregations of adults of both sexes are commonly recorded south of 45°S in summer-autumn, particularly in Grande Bay (Álvarez Colombo, M.S.). These are most likely supported by the co-occurring high copepod biomass regularly found in the area since this group normally dominate their diet (Gibbons *et al*., 1992).

Further hydrographic and fito-mesozooplankton research is at present being conducted in the region in order to characterise the plankton production cycle in relation to the occurrence of frontal structures and, eventually, to elucidate how this interplay affects higher trophic levels.

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