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Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species

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Seasonal zooplankton succession (mainly of the mesozooplankton) in the inner zone of Bahía Blanca estuary during the period 1990–1991 was compared to that from the period 1979–1980 in order to detect changes having taken place in 10 years. Taxonomic composition, zooplankton abundance, species occurrence and temperature–salinity conditions were studied within the two annual cycles. This estuarine ecosystem has been deeply affected by a population increase and by the rapid growth of industrial activity and maritime traffic over the last two decades. Several changes in the zooplankton assemblage composition and structure were detected, probably due to temperature–salinity gradient patterns, which showed discernible differences. Dominance, during winter–spring, of two new invading species, namely, the cirriped Balanus glandula and the copepod Eurytemora americana, causing a decrease in the autochthonous key copepod Acartia tonsa, was one of the principal features of the period 1990–1991. Seasonal changes in diversity and species richness, as well as differences in the multivariate general pattern of the zooplankton community structure with a consequent decrease in the community stability during the second period, were also observed.

INTRODUCTION

Seasonal plankton succession in estuaries is a process mainly regulated by temperature and salinity conditions, although bottom-up as well as top-down controls (i.e. available food production, grazing, competition and predation) also play an important role in this process (Knatz, 1978; Wooldridge and Melville-Smith, 1979; Bradley, 1990; Hoffmeyer, 1994; Calbet *et al.*, 2001). In addition, environmental changes may cause either short- or long-term effects on the plankton features.

The Bahía Blanca estuary ecosystem underwent a severe perturbation throughout the 1980s and 1990s as a result of increasing industrial activities, maritime traffic, dredging and pollution (Lara *et al.*, 1985; Villa, 1988), all of which affected, in particular, the innermost zone of the estuary. Linked to year-to-year natural variations and sampling temporally patchy variability, effects on zooplankton assemblages (e.g. on composition, structure and dynamics) which may have been introduced by these man-made changes were observed.

Plankton assemblages from the innermost zone of the estuary display a pattern that is similar in structure and spatial–seasonal dynamics (Hoffmeyer, 1983; Mianzán, 1987; Barría de Cao *et al.*, 1997; Pettigrosso *et al.*, 1997; M. S. Hoffmeyer, unpublished results). During the period 1979–1980, surface mesozooplankton were represented by 30 species (Hoffmeyer, 1983). *Acartia tonsa*, a key species in the plankton of this zone, was present in 100% of samples. A decade later, the copepod seasonal succession in surface water off Ing. White Port was characterized by a strong seasonal variation of *A. tonsa* and *Eurytemora americana* as dominant and co-dominant species, respectively (Hoffmeyer, 1994).

In this work, I report qualitative and quantitative changes in zooplankton assemblages from the innermost zone of Bahía Blanca estuary during the period 1990–1991. To this end, the seasonal zooplankton succession characteristics from the two annual cycles, i.e. 1990–1991 and 1979–1980, were compared. Results are discussed in relation to temperature–salinity conditions and

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increasing pollution in the study area. The evidence concerning (i) two newly introduced species (*E. americana* and *Balanus glandula*), which had become seasonally dominant late during winter–spring 1990–1991, and which produce an apparent impact on the native species *A. tonsa*, (ii) the seasonal changes in diversity and (iii) the increase in the multivariate community dispersion in hyperspace 1990–1991 all constitute important findings that are analyzed in this paper.

METHOD

The study area concerns the innermost zone of Bahía Blanca estuary (Figure 1). Ing. White Port is located in this now highly polluted area of the estuary. Temperature and salinity are in general vertically homogeneous, although a strong horizontal salinity gradient related to the increase in freshwater flow may sometimes be observed (Freije *et al.*, 1981; Píccolo and Perillo, 1990). A tendency to hypersalinity was registered during some summers. A large number of industrial as well as wastewater effluents from Bahía Blanca and Punta Alta cities, from the northwestern margin of this inner zone, are discharged into the estuary.

Two data sets of surface water zooplankton abundance (mainly mesozooplankton) and temperature–salinity were considered in this study. One of them was obtained from samples collected off Ing. White Port between July 1979 and August 1980, and the other from samples from the innermost estuarine zone collected between July 1990 and August 1991. The methods followed and the qualitative zooplankton data corresponding to the first period have already been reported by Hoffmeyer (Hoffmeyer, 1983). The data corresponding to the second period were extracted from Hoffmeyer's study (Hoffmeyer, 1994), which gathers other macro-meroplankton abundance data.

Shannon–Wiener's diversity (H') and Simpson's dominance (λ) indices were calculated (Pielou, 1975). F and Student's tests on log-transformed data of total species abundance as well as of species richness and temperature–salinity raw values were run. Multivariate methods were also applied using the software PRIMER-E®. The relationship between the multivariate pattern of both abiotic variable data and sample abundance data from two time data sets was analyzed with the Relate routine, which uses the average Spearman rank coefficient (ρ_{av}). The index of multivariate dispersion (IMD) was applied

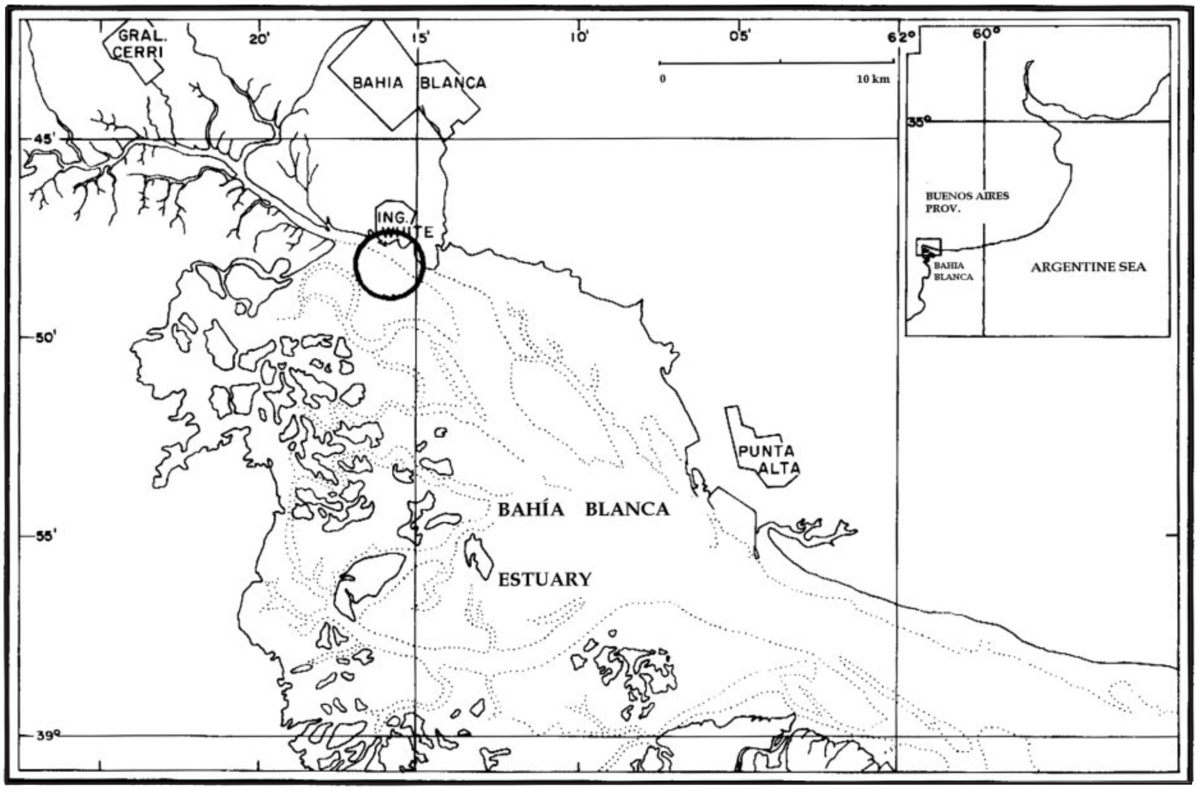

Fig. 1. Map of Bahía Blanca estuary showing the location of Ing. White Port, the sampling station.

as a multivariate stability index (MSI) to evaluate the stability changes in the community (Warwick and Clarke, 1993). Testing of the null hypothesis of no stability change under disturbance between two time data sets was performed following IMD analysis. The significance was estimated first by a permutation test and secondly by a Monte Carlo test (Hope, 1968; Clarke and Warwick, 1994). Finally, similarity percentages among the species within each group (1979–1980 and 1990–1991) and the dissimilarity percentage between the two data sets, plus each species' contribution to the latter, were estimated applying the Simper routine. In this case, rarer species (i.e. those that accounted for <2% of the total species abundance in each sample and occurrence values <10% for each annual period) were excluded (Clarke and Warwick, 1994).

RESULTS

Temperature–salinity conditions

Surface temperature values during 1979–1980 and 1990–1991 varied in a similar way (Figure 2, top). However, the differences registered in the present study consisted of a delay in the timing of maximal and minimal values during the summer–autumn–winter values of the

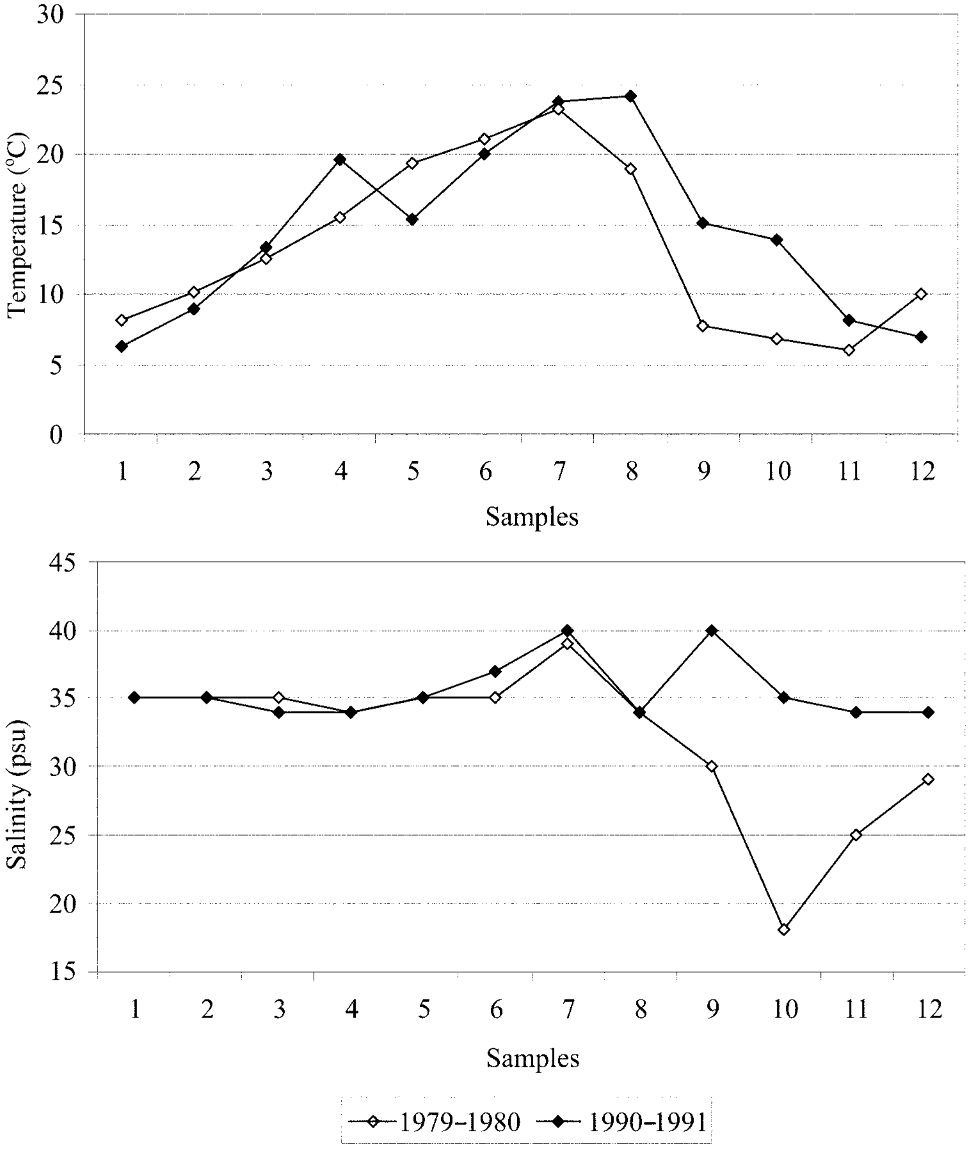

Fig. 2. Temperature (°C) curve (top) and salinity (psu) curve (bottom) corresponding to dates from the months of July to August (next year) of the 1979–1980 and 1990–1991 survey periods, at Ing. White Port.

1990–1991 curves with respect to that from the 1979–1980 period. Surface salinity values were highly variable during 1979–1980, with more lower values during autumn–winter than in summer as a result of the large freshwater run-off into the inner zone of the estuary during this period (Figure 2, bottom). As to the salinity values corresponding to the period 1990–1991, they were not so variable. In addition, a trend towards hypersalinity in summer was observed in both annual periods. Significant differences were only found for the salinity variance from both years ($P < 0.05$). However, through the Spearman rank coefficient (ρ) applied to two similarity matrices from both periods, a common multivariate pattern of temperature–salinity was determined. Nevertheless, temperature and salinity differences were discernible.

Zooplankton seasonal succession in 1979–1980

Acartia tonsa was the only species occurring throughout the whole year (100%) (Table I). There was an 80% occurrence of *E. acutifrons* and actinula larvae of the hydroid *Tubularia crocea*, a 40–50% occurrence of *Paracalanus parvus* and Grapsidae, and a 25–30% occurrence

Table I: Percentage occurrence (left) and abundance (right) values of species registered in the two annual cycles at Ing. White Port in Bahía Blanca estuary

Species	1979–1980		1990–1991	
	%	No. m^{-3}	%	No. m^{-3}
Acartia tonsa Dana, 1849	100	996.25	100	1257.92
Paracalanus parvus (Claus, 1863)	58	40.83	58	77.42
Labidocera fluviatilis Dahl, 1894	1	21.08	25	77.00
Calanoides carinatus Kröyer, 1848	1	11.08	25	43.08
Boeckella poopensis Marsh, 1906	17	5.92	–	–
Eurytemora americana Williams 1906	–	–	50	30.33
Oithona nana Giesbrecht, 1892	1	5.50	25	20.08
Euterpina acutifrons (Dana, 1847)	83	5.25	33	10.33
Tisbe varians T. Scott, 1914	25	5.17	17	10.00
Robertsonia propinqua (T. Scott, 1893)	17	4.67	–	–
Hetrolaophonte sp. (aff. *pauciseta*)	17	4.50	–	–
Nannopus palustres Brady 1880	1	3.67	–	–
Harpacticus chelifer (Müller) 1776	1	2.58	17	4.58
Dactylopodia tisboides (Claus, 1863)	1	2.25	–	–
Monstrilla helgolandica Claus, 1863	1	2.08	8	4.50
Monstrilla sp. (aff. *grandis*)	1	2.00	–	–
Daphnia spinulata Biraben, 1917	20	1.75	–	–
Peisos petrunkevitchi Burkenroad	17	1.75	–	–
Neomysis americana (S. I. Smith, 1873)	17	1.67	33	3.00
Arthromysis magellanica (Cunningham, 1871) (juv)	1	1.50	42	2.75
Sagitta friderici Ritter-Zahoni, 1911	1	1.08	17	2.08
Ciona intestinalis (Linnaeus), 1767 (tadpole larvae)	17	1.17	–	–
Ceriantharia (cerinula larvae)	17	1.08	17	2.08
Grapsidae (zoeae I–IV and megalopa larvae)	42	0.92	42	2.08
Balanus glandula Darwin (larvae)	–	–	42	1.33
Tubularia crocea Agassiz, 1862 (actinula larvae)	83	0.75	8	1.00
Bivalvia (veliger larvae)	17	0.75	42	0.83
Gastropoda (veliger larvae)	17	0.67	25	0.75
Bryozoa (cyphonautes larvae)	1	0.67	25	0.67
Spionidae (nectochaet larvae)	1	0.50	42	0.50
Brevoortia aurea Hildebrand, 1948 (eggs–larvae)	17	0.50	8	0.25
Atherinidae (larvae)	17	0.50	–	–

of *T. varians*, *Daphnia spinulata* and *Boeckella poopensis*. The remaining species showed a lower percentage occurrence. Total zooplankton abundance fluctuated from values >100 individuals (ind.) m^{-3} in November 1979 and higher in winter, to values >3000 ind. m^{-3} in April 1980. *Acartia tonsa* varied from ~100 ind. m^{-3} in June 1980 to almost 3000 ind. m^{-3} in April, being the most abundant zooplankton by one order of magnitude with respect to the remaining species throughout the whole year. The latter were, in decreasing order of abundance, *E. acutifrons*, Grapsidae larvae and *P. parvus*, with other species showing a much lower abundance.

The percentage share of those species contributing most to total abundance is shown in Figure 3 (left). Although present from winter to summer, *E. acutifrons* registered a peak in spring in association with intermediate temperatures, but was less abundant in summer. In winter 1980, an exceptional salinity gradient with a sharp decrease in values at the estuarine head and inner area, as a result of heavy precipitation throughout the region, produced the conspicuous occurrence of two freshwater forms: *D. spinulata* and *B. poopensis*. Grapsidae larvae, and to a lesser extent Gastropoda larvae, appeared during spring and their numbers increased in summer, from October to February, in relation to temperate and warm temperatures. In summer and autumn, *P. parvus* was also present, being more abundant in summer when the temperature was warmer. *Tisbe varians* showed a peak in May, diminishing during winter in both study periods. Small pulses of *Robertsonia propinqua* and *Harpacticus chelifer* were also observed in winter, obviously related to cold temperatures.

Zooplankton seasonal succession in 1990–1991

The abundance variation data were based on Hoffmeyer (Hoffmeyer, 1994) with the addition of new data on meroplankton. *Acartia tonsa* was again present throughout the whole year (100% occurrence), followed by the copepods *P. parvus* and *E. americana* with only 58% and 50% occurrence, respectively (Table I). An important group of species such as Grapsidae larvae, the mysids *Neomysis americana* and *Arthromysis magellanica*, and the copepod *E. acutifrons*, was observed in a 30–45% occurrence range. Other meroplankton and Copepoda species showed a 25% occurrence or a lower range. Total zooplankton abundance fluctuated from low values close to or higher than 100 ind. m^{-3} in July, October–November 1990 and August 1991 to values around 5000 ind. m^{-3} in May 1991. *Acartia tonsa* abundance varied from 3 ind. m^{-3} in July 1990 to around 4700 in January and 4900 ind. m^{-3} in May 1991, being the most abundant zooplankton in total over the year by one or two orders of magnitude. The remaining species, in descending order of abundance, were the larvae of *B. glandula*, the copepods *E. americana* and *E. acutifrons*, as well as Grapsidae and Spionidae larvae, with values ranging from around 100 to 700 ind. m^{-3}. All remaining species had a lower abundance.

The percentage values corresponding to the most abundant species during winter and spring are shown in Figure 3 (right). *Acartia tonsa* was present throughout the whole year, showing lower values than those during summer and autumn. *Eurytemora americana* and *B. glandula* larvae were registered from the end of June to October, giving rise to peaks in September and disappearing completely in October. Small peaks of Spionidae larvae, the mysids *N. americana* and *A. magellanica*, and typical copepods from the outer shelf area of the estuary such as *Labidocera fliviatilis*, *Calanoides carinatus* and *Oithona nana* were also found during winter and spring. The non-typical estuarine copepod *P. parvus* and larvae of Grapsidae were present during late spring, summer and autumn, with peaks in summer.

Seasonal succession comparison (1979–1980 and 1990–1991 periods)

Although some differences were observed in total species abundance, species richness and diversity–dominance pattern between the 2 years (Figure 4), significant differences were only found for total species abundance variance ($F = 0.34$, $P < 0.04$).

Comparison of the sample biotic similarity matrices showed a different pattern between years, whereas the IMD index (−0.41) indicates an increase in the community variability (stability) during the second period. The average similarity percentage among species was 47.46% during 1979–1980 against 35.97% during 1990–1991, the main species contributing were *A. tonsa* (73.39%), *E acutifrons* (9.61%), *T. crocea* larvae (5.89%) and *P. parvus* (4.17%) for the first year, and *A. tonsa* (69.65%), *E. americana (*5.52%), *P. parvus* (4.81%), Spionidae larvae (4.67%), *B. glandula* larvae (4.46%) and Grapsidae larvae (4.17%) for the second year. The average dissimilarity between sample sets was high (62.81%).

Table II shows the major changes in the composition of zooplankton assemblages after a decade. The main changes observed were the appearance and population increase of *B. glandula* and *E. americana*, the disappearance of *D. spinulata* and *B. poopensis* as a result of changes in salinity conditions in winter, the abundance increase of several outer species such as *P. parvus*, *A. magellanica* and *N. americana* probably as a result of a dredging effect, and a decrease or increase in abundance of larval forms from benthic species, probably due to community disturbance processes.

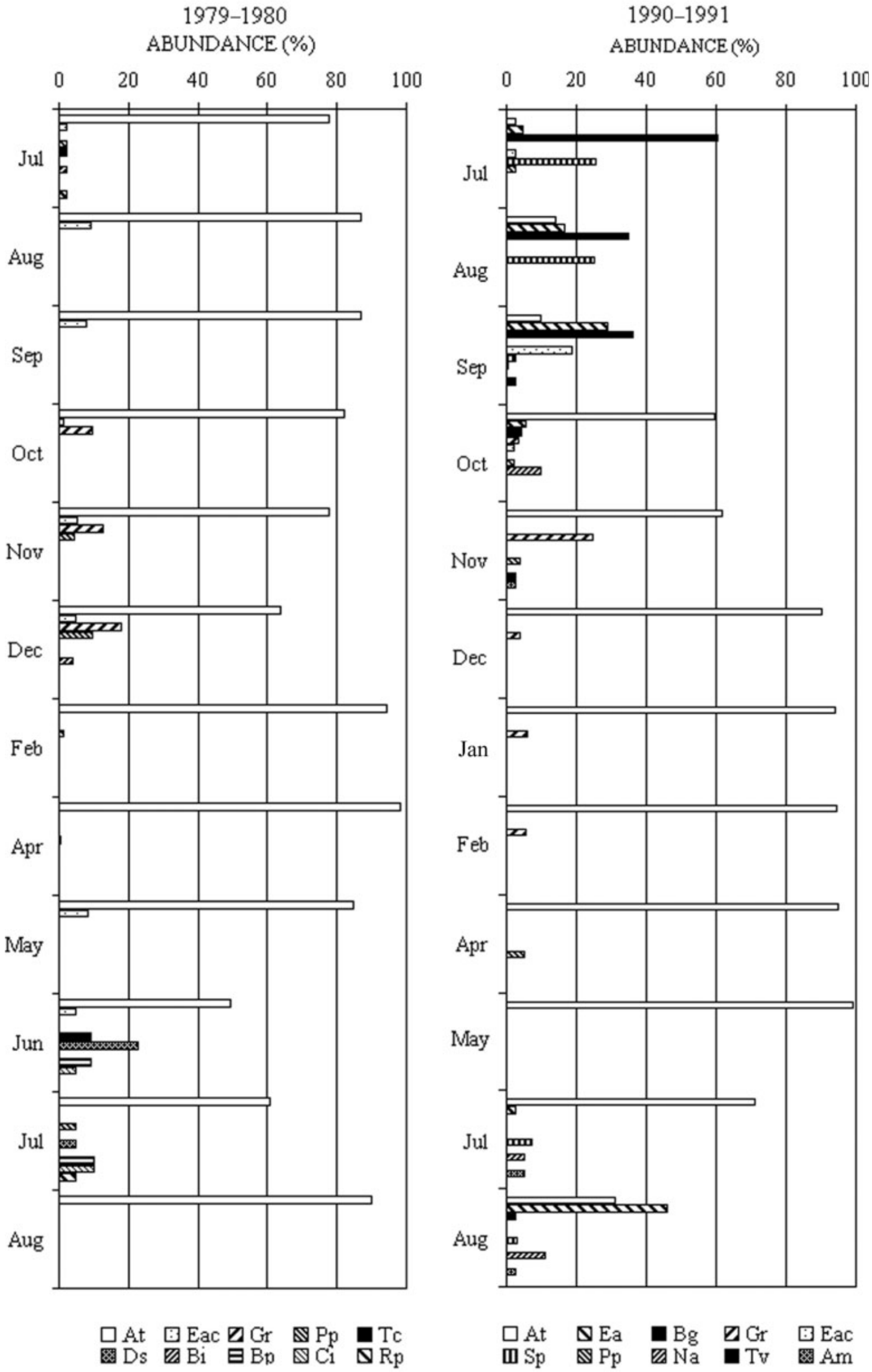

Fig. 3. Percentage abundance of the main species during the annual periods 1979–1980 and 1990–1991 (left and right, respectively). At, *Acartia tonsa*; E ac, *Euterpina acutifrons*; Gr, Grapsidae; Pp, *Paracalanus parvus*; Tc, *Tubularia crocea*; Ds, *Daphnia spinulata*; Bi, Bivalvia; Bp, *Boeckella poopensis*; Ci, *Ciona intestinalis*; Rp, *Robertsonia propinqua*; Ea, *Eurytemora americana*; Bg, *Balanus glandula*; Sp, Spionidae; Na, *Neomysis americana*; Tv, *Tisbe varians*; Am, *Arthromysis americana*.

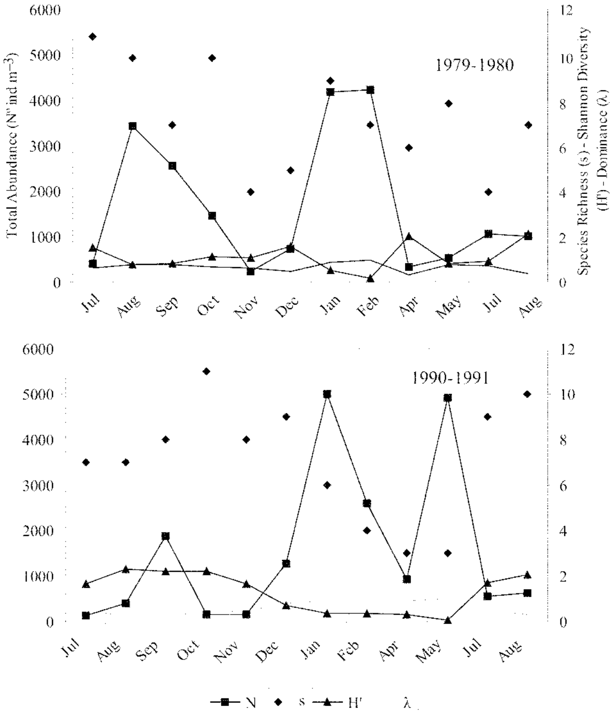

Fig. 4. Total zooplankton abundance, species richness (s), Shannon and Wiener's diversity index (H') and Simpson's dominance index (λ) values for the 1979–1980 (top) and 1990–1991 (bottom) periods.

DISCUSSION

Our results show the presence of two new species, *B. glandula* larvae (nauplii I–VI to cypris) and *E. americana*, with very high abundance values in 1990–1991, although they were absent in 1979–1980. *Balanus glandula*, a relatively new immigrant in the estuary, was observed in small numbers from the mid-1980s onwards. It was probably already present in 1979–1980, but remained undetected because of its low number. Its distribution later expanded southward along the coast of the Province of Buenos Aires (Spivak and L'Hoste, 1976; Orensanz *et al.*, 2002) and along the Patagonian coast, up to the port zone of Comodoro Rivadavia city (Rico *et al.*, 2001). Since its arrival in the Bahía Blanca estuary, the population grew rapidly, competing successfully for space with *B. a. amphitrite* (the other cirriped species) within the inner estuary to the estuary head (Wagner *et al.*, 1993; M. S. Hoffmeyer, unpublished results). The other invading species, *E. americana*, was also observed for the first time in the mid-1980s. Each year, this copepod remains in the plankton for around 4 months and then disappears, this being a phenomenon related to the strategy of diapause egg production (Marcus *et al.*, 1994). *Eurytemora americana* is a copepod regularly found in several estuaries from the northern hemisphere, and it may have been accidentally introduced into Bahía Blanca estuary via ballast water from ships (Hoffmeyer, 1994; Hoffmeyer *et al.*, 2000). From its arrival, the *E. americana* population has increased in density over the years, co-existing with *A. tonsa* during its planktonic pulse (June–July to October), but producing a slight exclusion of this copepod. This was demonstrated by the increase in abundance of *E. americana* in 1990, coinciding with a decrease in *A. tonsa* abundance [(Hoffmeyer, 1994); Figure 3)]. During September 1990, *E. americana* reached an abundance value that was 5-fold that of *A. tonsa*. This temporal exclusion of the *A. tonsa* population is probably due to two control processes. One such process is the overlapping of their trophic niches, with *E. americana* having the advantage of being better adapted to feed more efficiently on phytoplankton from the winter–spring bloom than *A. tonsa*, as inferred by Hoffmeyer and Prado Figueroa on the basis of the differences in the integumental structures observed in the oral field of both copepods (Hoffmeyer and Prado Figueroa, 1997). The other control process could be the selective predation on *A. tonsa* by planktonic carnivores such as ctenophores, fish larvae or chaetognaths, a phenomenon that has not been studied to date.

From a quantitative point of view, there were a few species with the same overall seasonal abundance variation pattern during the two periods studied. Although *A. tonsa* showed overall dominance during both periods, in 1979–1980 it was dominant throughout the whole year, whereas in 1990–1991 it was dominant only from October to July. In 1979–1980, *A. tonsa* accounted for ~50–100% of total zooplankton, in mean terms (see Figure 3). In 1990–1991, conversely, its abundances ranged from 60% to almost 100%, but only between October and July. In both periods, the minimum abundance of this species during winter suggests resting egg production. This reproductive strategy had already been suggested as possible in *A. tonsa* in the inner zone of Bahía Blanca estuary by Sabatini (Sabatini, 1989). Grapsidae larvae were the main component of the meroplankton, showing a similar variation trend in the two periods during the spring–summer months and an increase in abundance in 1990–1991. There is a very marked difference in the timing of *A. tonsa* and Grapsidae peak zones in the seasonal abundance curves between the first and second periods. *Acartia tonsa* gave rise to a bimodal curve in 1979–1980, which became a unimodal curve in 1990–1991. Grapsidae larvae showed a peak in December 1979, which was also shown in November 1990. Interestingly, the timing of the planktonic pulse of these larvae was similar. The seasonal distribution of these larvae displayed the same trend between March 1983

Table II: Major changes produced in the structure and composition of the zooplankton community and possible causes

Species	Changes		Causes
	% ocurrence	Abundance	
Paracalanus parvus	Equal	Increase	Dredging
Labidocera fluviatilis	Increase	Increase	Dredging
Calanoides carinatus	Increase	Increase	Dredging
Boeckella poopensis	Decrease	Decrease	Winter salinity
Eurytemora americana	Increase	Increase	Introduction
Oithona nana	Decrease	Decrease	Dredging
Robertsonia propinqua	Decrease	Decrease	Dredging
Hetrolaophonte sp.	Decrease	Decrease	Benthos changes
Nannopus palustris	Decrease	Decrease	Benthos changes
Harpacticus chelifer	Increase	Increase	Benthos changes
Monstrilla helgolandica	Increase	Increase	Benthos changes
Monstrilla sp. (aff. *grandis*)	Decrease	Decrease	Benthos changes
Daphnia spinulata	Decrease	Decrease	Winter salinity
Peisos petrunkevitchi	Decrease	Decrease	?
Arthromysis magellanica	Increase	Increase	Dredging
Sagitta friderici	Increase	Increase	Dredging
Ciona intestinalis (tadpole larvae)	Decrease	Decrease	Benthos changes
Balanus glandula (larvae)	Increase	Increase	Benthos changes
Tubularia crocea (actinula larvae)	Decrease	Increase	Benthos changes
Bryozoa (cyphonautes larvae)	Increase	Increase	Benthos changes
Spionidae (nectochaet larvae)	Increase	Increase	Benthos changes
Atherinidae (larvae)	Decrease	Decrease	?

and November 1985 (Cervellini, 1992). Changes in timing were also observed in the abundance curves of other species such as the copepods *E. acutifrons* and *P. parvus* (a typical species from the outer estuarine and shelf zones), and Spionidae larvae, which were much more abundant during the second period (1990–1991).

The marked differences in the community structure found between the two periods (i.e. diversity–dominance, species richness, total species abundance) seem more likely to be due to the presence of two new species in 1990–1991 and to differences in the timing and abundance of other assemblages, rather than to differences in the abiotic multivariate pattern (temperature–salinity), on account of the fact that the latter did not differ significantly from one period to the next. The species contributing most to the average dissimilarity (62.81%) in the community structure of the two periods are the autochthonous species *A. tonsa* (a 30% contribution), *E. acutifrons* and Grapsidae larvae (7–7.5%), the new invading species *E. americana* and *B. glandula* (6–7%) and Spionidae larvae (almost 5%). On the other hand, the main quantitative and qualitative differences in the zooplankton structure of the two annual cycles were more strongly observed in the period winter–spring than in the period summer–fall.

However, the significant differences observed in salinity variance show a sharp decrease in the values with an increase in the horizontal salt gradient during winter 1980 (June, July). The very high seasonal abundance of *D. spinulata* and *B. poopensis*, both freshwater forms, testifies to the marked increase in run-off in the inner zone of the estuary.

In view of the above-mentioned results, it can be concluded that a conspicuous change in the multivariate pattern occurred from one decade to the next, the species responsible for this change being identified in the present study. The decrease in community stability in the second period (1990–1991) may be considered a reflection of the environmental disturbance. Although, apparently, the zooplankton community displayed a similar pattern between the 2 years, important changes in zooplankton composition after 10 years were detected. They may be the result of natural year-to-year variability (modified to a greater or lesser extent by the effects of global change) combined with man-induced changes at the local level. Since this estuary is shallow and mixed, the plankton–benthos coupling is apparently very strong, so that dredging and its effects on the benthos community could also have strongly affected the plankton community.

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