MARINE LIFE OF URUGUAY: CRITICAL UPDATE AND PRIORITIES FOR FUTURE RESEARCH

LA VIDA MARINA DE URUGUAY: REVISION CRITICA Y PRIORIDADES PARA INVESTIGACIONES FUTURAS

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ABSTRACT

The marine areas of Uruguay consist of the Río de la Plata estuary and the adjacent shelf and slope, part of the Sub-tropical Convergence Ecosystem. In this paper, the main advances in the knowledge of marine life in these areas (the known) are reviewed in order to discuss future lines of research (the unknown). Information has been separately analysed for the plankton, nekton, and benthos in each of 3 areas-the littoral, the shelves and the "open ocean". Current knowledge of marine life is uneven among the groups and areas. In the case of the plankton, research has concentrated on the near-shore waters and focused on taxonomy and distribution. Little is known about the responses of organisms to environmental variability and about biological processes. The nekton of coastal and estuarine areas is better known, but, with shelf and slope assemblages, research has focused on exploited species. The main unknowns for the nekton are how trophodynamics, reproduction, and recruitment processes are linked to environmental variability and the effect of fisheries on community structure. Littoral benthos, in particular the macroinfauna of sandy beaches, is much better studied and spatial patterns of community distribution have been identified at different scales and in relation to environmental variables. Also, at the population level, there is information about distribution, responses to disturbances, dynamics, and the roles of biotic and abiotic factors in modulating population variability. Information is mainly lacking for the sub-tidal fringe and regarding the macro-ecology of population dynamics, the dispersive abilities of larval phases, and the effects of toxic blooms on suspension feeders. Knowledge of the benthos of estuaries and more so of the shelf and slope environments is rather scarce. For the latter two, faunal inventories are far from complete. Topics identified for future research include taxonomy, macro-scale community structure and its temporal variability in relation to environmental gradients, diverse aspects of population dynamics trophodynamics and the effects of human intervention on ecosystems. The incorporation of both experimental and modelling approaches is considered important for future investigations.

KEYWORDS: Marine life; Biodiversity; Río de la Plata; Atlantic Ocean, Uruguay.

RESUMEN

Las aguas uruguayas comprenden el estuario del Río de la Plata y la plataforma y talud contiguos, parte del Ecosistema de Convergencia Subtropical. Esta contribución revisa los principales avances en el conocimiento de la vida marina en esta zona (lo conocido), para discutir futuras líneas de investigación (lo desconocido). Se analiza separadamente la información del plancton, necton y bentos de tres áreas: litoral, plataforma y "océano profundo". El conocimiento resulta dispar entre grupos y entre áreas. En el plancton, la investigación se concentró en el litoral y enfocada hacia

aspectos taxonómicos y de distribución, existiendo fuertes deficiencias en el conocimiento de las respuestas de los organismos a la variabilidad ambiental y de procesos biológicos. El necton de áreas estuarinas y costeras es mejor conocido que el de plataforma y talud, donde la investigación ha sido dirigida principalmente a especies explotadas. En este grupo, los principales aspectos desconocidos son los trofodinámicos, los procesos reproductivos y de reclutamiento en función de la variabilidad ambiental, y el efecto de las pesquerías sobre la estructura comunitaria. El bentos litoral, en particular la macroinfauna de playas arenosas, es el componente mejor conocido: se han establecido patrones de distribución comunitaria en diferentes escalas espaciales y en relación a variables ambientales. A nivel poblacional existe información sobre distribución, repuesta a perturbaciones, dinámica, y sobre el papel de factores bióticos y abióticos en la modulación de la variabilidad poblacional. La información faltante se refiere a la franja submareal, así como a aspectos macro ecológicos de dinámica poblacional, dispersión larval y el efecto de las floraciones tóxicas sobre organismos suspensívoros. El bentos de estuarios, y en particular aquél de plataforma y talud, es muy poco conocido; para los últimos los inventarios faunísticos son extremadamente incompletos. Los tópicos identificados para próximas investigaciones incluyen taxonomía, la estructura de las comunidades y su variabilidad temporal en gradientes ambientales, diversos aspectos de dinámica poblacional, trofodinámica y el efecto de la intervención humana en los ecosistemas. Se considera muy importante la incorporación de enfoques experimentales y modelización.

PALABRAS CLAVES: Vida Marina; Biodiversidad; Río de la Plata, Océano Atlántico; Uruguay.

INTRODUCTION

The marine domain of Uruguay is made up of the Río de la Plata and the adjacent shelf (Fig. 1) and shares ecosystems with Brazil and Argentina. Present understanding of the distribution of marine life and related ecological processes in the region is owed to contributions from local, regional, and international scientific communities. Knowledge is still rather limited, however, partially because some ecosystems have not been adequately investigated. Reviews (Méndez *et al.* 1997, Seeliger *et al.* 1997, Mianzán *et al.* 2000) about these and adjacent ecosystems have proved to be particularly useful because a large amount of the information produced so far is highly dispersed and not readily available as it is published in Journals of limited circulation or as technical reports. This paper updates the main advances regarding marine biota in order to identify future lines of research for Uruguay. It first summarizes the most conspicuous physical characteristics of the area, then, for each group (plankton, nekton, and benthos) and critically reviews what has been done to provide our current understanding of the distribution and dynamics of marine life (the known), with emphasis on the contributions from Uruguayan scientists. Finally, it discusses research priorities (the unknown) in the light of what is known.

The waters off Uruguay can be divided into two broad systems, the Río de la Plata (RdIP) and its

zone of influence over the inner continental shelf, and the shelf/shelf-break ecosystem. They include a large coastal, estuarine influenced area, a wide continental shelf, and a slope and deep basin where the confluence of the Brazil Current (BC) and Falkland (Malvinas) Current (FC) takes place (Atlantic Subtropical Convergence).

The RdIP is a funnel-shaped, coastal plain, microtidal estuary situated at 34°10' - 36°10' S, 55°00' - 58°10' W. It is 200 km long and 230 km wide at the mouth between Punta del Este (Uruguay) and Cabo San Antonio (Argentina), with a surface area of ca. 38,000 km². The main tributaries are the Paraná-Paraguay and Uruguay rivers, which drain the second largest basin in South America (Framiñan & Brown 1996, Nagy *et al.* 1997) and provide the major source of freshwater runoff in the southwest Atlantic.

The upper estuary has very low salinities (<1‰) and extremely turbid waters, whereas the lower estuary is somewhat less turbid with highly variable salinity in space and time (1-33‰) strongly influenced by Atlantic Coastal Waters (a combination of BC, FC, and freshwaters from continental runoff (Guerrero *et al.* 1997). Upper and lower regions are separated by a salinity front –the upper reach of the salt wedge– and a turbidity front that almost overlap and present complex and variable geometries (Framiñan & Brown 1996, Guerrero *et al.* 1997). Marine waters penetrate in the form of a salt wedge, and the characteristics of the

gradients are dependent upon wind intensity and direction, freshwater runoff, and bottom topography (Guerrero *et al.* 1997, Nagy *et al.* 1997). The depth is less than 10 m over > 50% of its surface area with a maximum of *ca.* 25 m at the mouth.

In the upper estuary, bottom topography is characterised by a system of channels and banks, and sediments are composed of fine fractions, mainly silts and clays (López 1997). The Barra del Indio

bank separates the upper estuary, dominated by extensive shallows (1-4 m deep, i.e. Playa Honda, Banco Ortiz) and coastal channels (5-8 m deep, Canal Oriental Oeste, Canal Intermedio), from the lower estuary. The latter is wider and deeper, which allows the development of a vertical structure in the water column (Framiñan & Brown 1996), and the sediments are predominantly relict sands (López 1997).

FIGURE 1. Map of Uruguayan waters, including the Río de la Plata waters shared with Argentina. Also indicated are major geographic references mentioned in the text.

FIGURA 1. Mapa de las aguas Uruguayas, incluyendo aquellas del Río de la Plata compartidas con Argentina. Se indican también las principales referencias geográficas mencionadas en el texto.

The offshore environment is dominated by 2 major boundary currents, the poleward flowing BC and the equatorward FC. They appear as tongue-like structures that 'collide' off the RdIP, the former being deflected offshore while the latter slides inshore (Olson *et al.* 1988, Bakun & Parrish 1991). Over the shelf, there is an onshore-offshore transition from continental influenced waters (Coastal Waters, CW) to Central Atlantic Waters (CAW). The inner shelf is occupied by CW, a mixture of CAW and freshwater outflow from the RdIP and Patos Lagoon (Ciotti *et al.* 1995, García 1997). The plume of the RdIP moves NNE as a shallow surface layer along the Uruguayan coast in the austral autumn/winter but southwards along the Argentinian coast in the spring/summer, the direction being determined by the balance between on- and offshore winds (Guerrero *et al.* 1997). The plume of RdIP brackish water over the shelf induces a fairly stable density profile (Castello & Müller 1977, Bakun & Parrish 1991).

Further offshore, surface CAW results from the mixing of FC and BC waters between 25°S and 45°S (Olson *et al.* 1988, Garzoli & Garrafo 1989, Gordon 1989, Bianchi *et al.* 1993, Odebrecht & Castello 2000). BC water is warm, saline, and relatively oligotrophic (Bisbal 1995). It is a branch of the South Equatorial Current and flows poleward nearly parallel to the shelf-break. The cool, nutrient-rich FC branches off the Antarctic Circumpolar Current (ACC) flowing northward along the continental slope. The confluence of the BC and FC results in complex meso-scale circulation patterns like warm or cold-core rings, eddies, and filaments (Legeckis & Gordon 1982, Olson *et al.* 1988, Gayoso & Podestá 1996). The zone between 30°S and 40°S has a high variability in physical and chemical properties and represents an ecotone of high biological diversity. Peaks of phytoplankton biomass have been found associated with frontal structures (Gayoso & Podestá 1996).

Biological information from two main sources has been reviewed: 1) Papers published in local, regional, or international journals, and 2) Recently updated bibliographic databases related to this area (López *et al.* 1999). In addition, the present authors' knowledge of antecedents and that deriving from discussions with colleagues on relevant published and unpublished information have also been used to some extent.

The information for the plankton, nekton and benthos in each of the 3 main areas, the littoral (supralittoral to 10 m depth), shelf (10–200 m), and "open ocean" (> 200 m), is reported separately. For the benthos, the littoral zone was further divided into sandy and rocky shores, in view of the significant research effort derived from these ecosystems in Uruguay.

Nomenclature follows Boltovskoy *et al.* (1999) for plankton and Cousseau *et al.* (1998) and Ponce de León (2000) for nekton.

THE KNOWN

PLANKTON

The South Atlantic Ocean hosts 50-100% of known zooplankton species, depending on the taxa considered. However, for a few groups (the Copepoda, Mysidacea, and Acantharia), the fraction is lower (<25%) (Boltovskoy *et al.* 1999). Between ca. 30°S and 45°S, the confluence of BC and FC results in a biogeographic Transition Zone off Uruguay which affects the large scale distribution pattern of most marine organisms (Boltovskoy *et al.* 1999). The occurrence of warm and cold water biota results in a somewhat lower diversity for taxa such as the Foraminifera, Chaetognatha, Salpida, Appendicularia, and Ostracoda, which is a deviation from the usual pattern of higher diversity at lower latitudes (Boltovskoy *et al.* 1999, Woodd-Walker *et al.* 2002).

Taxonomic studies and descriptions of the distribution in space/time have been the most frequent investigations in this area, in contrast to biological and process-oriented studies. Research efforts have been mostly directed towards the coastal areas. About 50% of the published studies were carried out in the nearshore area (<10 m), while the remaining 50% were conducted over the shelf, shelf-break, or deeper waters. The majority of the studies developed by Uruguayan scientists were in shallow waters; those at depths >10m were undertaken mostly by research groups from neighboring countries.

Coastal plankton: Euryhaline diatoms and dinoflagellates dominate the phytoplankton community in mixohaline and polyhaline waters, whereas, in fresh and oligohaline areas of the RdIP, the

Chlorophyceae and Cyanophyceae are also important; among the latter, *Microcystis aeruginosa* forms harmful algal blooms (De Leon & Yunes 2001). Phytoplankton biomass is highly variable (0.32-15.0 mg chl-a.l⁻¹) (Bazigaluz 1981, Cervetto *et al.* 2002), and is presumed to respond to changes in nutrient / light gradients modulated by the mixing of fresh and marine waters. A sharp reduction in turbidity (turbidity front) occurs just downstream from the upper reach of the salt wedge. The highest rate of phytoplankton production can be expected to occur seaward of the turbidity front as a result of improved light availability (Blanco 1989). This zonation within the RdIP is also reflected in the microplankton community structure (Souto 1974). Recent estimates by Gómez *et al.* (2001) suggest moderate to high productivity levels strongly influenced by the light regime.

In the coastal zone outside the influence of the RdIP, research on phytoplankton has been conducted in the Laguna de Rocha, an extremely shallow coastal lagoon. Studies have dealt with taxonomy and distribution in space/time (Conde *et al.* 1999), paleoecological reconstruction based on diatom assemblages (García *et al.* 2001, 2002, García & Witkowski 2002), and rate-process and functional studies involving light, nutrients, and UV modulation of primary production. Phytoplankton, epiphyton, and phytobenthos contribute to the high production of this ecosystem, the phytoplankton being the most efficient in terms of photosynthetic efficiency. Lagoon/ocean water exchange affects the optical characteristics and nutrient content of the water altering the limiting factors for primary production and modulating UV penetration in the water column (Conde 2001, Conde *et al.* 2002).

The few zooplankton studies conducted within the RdIP indicate a low diversity dominated by small copepods (*Acartia tonsa*, *Paracalanus parvus*, *Parvocalanus crassirostris*, *Oithona* spp.), mysids (*Neomysis americana*), and gelatinous plankton (ctenophores *Mnemiopsis maccrady* and *Liriope tetraphylla*) (González 1972, Milstein & Juanicó 1985). Ctenophores dominate macroplankton biomass during the warm season, and tend to aggregate near the mouth of the estuary at the surface salinity front where, has been suggested, they play an important trophic role (Mianzán *et al.* 1996, Mianzán & Guerrero 2000). Species richness tends to increase from Montevideo (salinity range 3-10;

Guerrero *et al.* 1997, Nagy *et al.* 1997) to Punta del Este (salinity range 20-30) with the addition of taxa like chaetognaths (*Saggita friderici*, *S. bipunctata*, *S. helenae*, and *S. hispida*), cladocerans (*Podon polyphemoides*, *Evadne normandii*) and copepods (*Ctenocalanus* spp., *Euterpina acutifrons*, *Centropages velificatus*, plus others) (Milstein & Juanicó 1985, Bastreri *et al.* 1988 (Fig. 2). This spatial pattern is likely to be highly dynamic and associated with the mixing and advection of water masses over short time-scales (i.e. hourly to fortnightly), as found for the Solís Grande river estuary, a sub estuary of the RdIP. There, a time-intensive sampling design showed a community dominated by a few copepod species (Cervetto 1987), controlled mainly by large scale physical forcing on a 15 day scale determined by the dominant wind pattern (Gómez *et al.* 2000) and by biological rhythms on a diel scale (vertical migration) (Calliari *et al.* 2001).

RdIP waters of Uruguay are also important spawning and nursery areas for several fish species. Plankton studies and analysis of the gonadal cycle of adult individuals indicate that the estuarine frontal zone close to the Uruguayan coast is probably the most significant spawning area for the white croaker (*Micropogonias furnieri*) and menhaden (*Brevoortia aurea*) (Macchi *et al.* 1996, Macchi 1997, Acuña *et al.* 1997, Vizziano 2001, see Mianzán *et al.* 2000). Nursery areas seem to be located very close to the coast, e.g. in the surf zone of sandy beaches or bays and small sub-estuaries (Martínez & Retta 2001). The saline frontal structure could provide a retention mechanism for larvae similar to that proposed for other areas (Sinclair 1988, Sinclair & Iles 1989) but the retention/advection mechanisms are still largely unknown, as are as most aspects of larval ecology. Deeper areas of the RdIP and inner shelf are spawning grounds for other estuarine-related commercial fishes like *Cynoscion guatucupa*, *Macrodon ancylodon*, and *Brevoortia* sp. (Hubold & Ehrlich 1981, Acuña & Viana 2001).

Shelf and open ocean: Knowledge of the plankton of shelf seas and shelf-break waters is similar to that described for the coastal region, though some general mechanisms have been proposed to relate phytoplankton development to the fertilizing effect of circulation patterns (see review in Odebretch & Castello 2000). In addition to the taxonomic stud-

ies of microplankton and phytoplankton groups (Müller-Melchers 1959, Balech & Souto 1980a, b, Akselman 1985, Lange & Mostajo 1985), a limited number of investigations have dealt with the relation between community structure and environmental conditions (Elgue *et al.* 1987, 1990, Negri *et al.* 1988, Mesones 1991, Gayoso 1996, Gayoso & Podestá 1996). The distribution of the phytoplankton assemblage off the RdIP follows a zonation pattern that reflects the mixing of water masses with differing nutrient contents along a coast-ocean gradient (Negri *et al.* 1988): an estuarine-influenced community immediately offshore from the RdIP is followed by coastal, transition, and subantarctic assemblages. This highly dynamic pattern is linked to the hydrographic variability, a view supported by the dominance of diatoms (Mesones 1991) or di-

noflagellates and cocolithophorids (Gayoso 1996) at different times in the same area. Shelf waters may host high phytoplankton biomasses (up to ca. 10 mg.l⁻¹ (Negri *et al.* 1988, Mesones 1991), and harmful algal blooms have been reported over wide areas of the shelf (Negri *et al.* 1992, Brazeiro *et al.* 1997). Over the outer shelf and slope, the interplay of BC and FC determines the hydrography and the characteristics of the biota (Boltovskoy *et al.* 1999 and references therein). Diatoms (*Thalassiosira*, *Lauderia*, and *Chaetoceros*), dinoflagellates (*Gymnodinium*, *Polikiros*, *Gyrodinium*), and unidentified flagellates dominate the phytoplankton, and their abundance seems to be strongly coupled to surface fronts and hydrographic features like eddies, filaments, and meanders created by the mixing of BC and FC (Gayoso & Podestá 1996).

FIGURE 2. Mean number of copepod species and salinity recorded at two sites over the salinity gradient of the Río de la Plata: Montevideo and Bahía Maldonado (Punta del Este). Data from Montevideo are from Cervetto *et al.* (1988) and data from Bahía Maldonado are from Milstein & Juanico (1985).

FIGURA 2. Número promedio de especies de copépodos y salinidad registrados en dos sitios a lo largo del gradiente salino del Río de la Plata: Montevideo y Bahía Maldonado. Los datos de Montevideo son tomados de Cervetto *et al.* (1988) y los de Bahía Maldonado son tomados de Milstein & Juanico (1985).

According to the synthesis by Odebrecht & García (1997) and Odebrecht & Castello (2000), continental runoff (from Lagoa dos Patos and RdIP) and turbulence over shallow waters control nutrient inputs to the inner shelf (Ciotti *et al.* 1995, Odebrecht & Djurfeldt 1996). This influences phytoplankton development which, during the productive season, reduces the nutrient levels seaward of the chlorophyll maximum (Negri *et al.* 1992, Abreu *et al.* 1995,

Ciotti *et al.* 1995). Over the outer shelf, fertilization is mainly due to the upwelling of nutrient-rich SAW caused by wind-driven cyclonic vortices, shelf and slope topography, and current shear (Hubold 1980a, b, García 1997, Odebrecht & Castello 2000), which enhance primary production (Niencheski & Fillmann 1997, Odebrecht & García 1997) and abundance (Gayoso & Podestá 1996).

Taxonomic approaches and spatial patterns in the

distribution of assemblages were the focii of zooplankton investigations (i.e. Esnal 1970, 1978, Ramírez 1970, 1973, Montero 1975, Ramírez & Zamponi 1980, Boltovskoy 1973, Goberna 1986, 1988, Gómez 1987, Amaral *et al.* 1997). The shelf zooplankton, dominated by copepods, is more species-rich than the coastal and estuarine populations. In-depth taxonomic reviews of most groups can be found in Boltovskoy *et al.* (1999). Distribution studies have mainly involved copepods and the results appear to be consistent with the phytoplankton zonation pattern referred to earlier (Fernández *et al.* 1994, Santos & Ramírez 1991). Both copepod and phytoplankton distributions reflect the various water masses present as described by Carreto *et al.* (1986). An increase in individual copepod size from the coast to the open ocean has been documented (Fernández *et al.* 1994); this probably results from changes in species composition over that gradient. At the southern end of the Brazilian shelf (27–35°S), Resgalla *et al.* (2001) found that zooplankton was affected by offshore Ekman transport and that the highest biomass occurred off the southernmost coast during summer and autumn. Biomass peaks corresponded to gelatinous plankton (mainly salps) whose low energetic value, high grazing capabilities, and significant contribution to the downward export of organic matter could strongly influence the structure of the pelagic ecosystem (Montú 1997, Resgalla *et al.* 2001). A preliminary assessment also suggested that zooplankton is a major food source for the juveniles of many fish species (Goberna 1987). The ichthyoplankton of the shelf and shelf-break waters is rather rich, comprising about 88 species (Sinque & Muelbert 1997). Most efforts have been directed towards describing the distribution and general ecology of *Engraulis anchoita*, the dominant small pelagic species, and *Merluccius hubbsi*, the major demersal fishery resource. Spawning grounds of these species are associated with frontal areas (Mantero 1986, Ciechomski & Sánchez 1986, Ehrlich & Ciechomski 1994, Ehrlich 2000). *E. anchoita* in particular is probably the better studied species in relation to different aspects of its early life stages (Sánchez 1991). Ichthyoplankton studies were also conducted with other clupeoids (*Brevoortia pectinata*, *Anchoa mitchilli*, *Lycengraulis grossidens*; Weiss *et al.* 1976, Weiss & Souza 1977, Hubold & Ehrlich 1981), Stomiiformes (Bonecker

& Hubold 1990), and Myctophidae (Sinque & Muelbert 1997).

NEKTON

The first studies of the ichthyofauna of the RdIP and adjacent waters were performed by Holmberg (1888), Berg (1895), Devincenzi (1920a, 1920b, 1924, 1933, 1939a, 1939b), Devincenzi & Barattini (1926, 1928), Devincenzi & Legrand (1936, 1940), and De Buen (1950). A systematic key and extensive list of species were published by Ringuelet & Aramburu (1960) and Menni *et al.* (1984). A complete list of fish species present permanently or occasionally in the area (360 species) has been provided by Cousseau *et al.* (1998).

The fish assemblages of the RdIP and its oceanic front are parts of those present along the continental shelf and slope between 34°S and 38°S at up to 1.000 m depth. The ichthyofauna inhabiting this area result from the influence of the 2 main zoogeographic provinces in the Southwestern Atlantic - Magellanic (subantarctic) and Argentinian (subtropical) (López 1963, 1964, Menni 1983, Menni & López 1984, Menni & Stehmann 2000) - which exhibit a large spatio-temporal variability during the year.

Río de la Plata and coastal waters. On the basis on 4 research cruises, Cousseau (1985) classified the fish of the RdIP according to their environmental preferences as freshwater (n=7), stenohaline (n=19), and euryhaline (n=58) species. More recently, Nión (1998), using bibliographic surveys and the results of cruises, suggested that, in the RdIP, there are 174 freshwater species, 53 marine species, and 42 visiting marine species. The most abundant species which constitute the basis for important fisheries in the region undergo seasonal trophic or reproductive migrations related to changes in the hydrographic conditions (Bellisio *et al.* 1979, Ciechomski *et al.* 1979, Cousseau *et al.* 1979, 1986, Ehrhardt *et al.* 1977a, 1979, Nión 1985, Ubal 1986, Otero 1986, Otero *et al.* 1982, 1986, Rey & Grunwaldt 1986, Arena *et al.* 1986, Fernández & Norbis 1986, Simonazzi & Otero 1986, Angelescu & Prenskey 1987, Ubal *et al.* 1987a, 1987b, Acuña *et al.* 1992, Norbis *et al.* 1992, Norbis & Galli 1999). The distribution, abundance, and population structure of chondrichthyes were analyzed by Meneses (1999) and Paesch (1999) for the RdIP and continental shelf, respectively.

Shark fisheries analyses were reported by Arena *et al.* (1974), Marín and Puig (1986) and Nión (1999) and the composition of catches and effects of longline fisheries on pelagic sharks have been described by Marín *et al.* (1998), Domingo (2000), Domingo *et al.* (1996, 2002) and Hazin *et al.* (in press).

In the coastal zone, teleosts of the family Sciaenidae (*Micropogonias furnieri*, *Cynoscion guatucupa*, and *Macrodon ancylodon*) are dominant out to a depth of 50 m. Abella *et al.* (1979) found 7 species in the rocky intertidal zone and in sandy beaches, with 2 species in common, *Micropogonias furnieri* and *Pogonias cromis*. Nión (1985) argued that the coastal system provides the principal nursery grounds for the former. The main coastal species spawn from October to March along the Uruguayan coast. Histological analysis showed that they do so seasonally, partially spawning with group-synchronised ovarian maturation (Arena & Hertl 1983, Vizziano & Berois 1990, Pravia *et al.* 1995, Macchi & Christiansen 1992, 1996, Macchi *et al.* 1996, Acuña *et al.* 1997, Acuña *et al.*, 2000; Viana *et al.*, 2000) which, in turn, is related to environmental variability (Acuña & Viana 2001, Vizziano 2001; Vizziano *et al.* 2001).

Shelf and open ocean. The species *Merluccius hubbsi*, *Cheilodactylus bergi*, and *Helicolenus dactylopterus lahillei* are the most abundant resources between 50 and 400 m depth. The hake (*M. hubbsi*) and the hawkfish (*C. bergi*) seasonally migrate in relation to changes in the oceanographic conditions, spawning during autumn/winter on grounds in the Argentinian-Uruguayan Common Fishing Zone (Ciechomski & Weiss 1974, Ehrhardt *et al.* 1977a, 1979; Grundwaldt 1986, Erlich & Ciechomski 1986, Christiansen *et al.* 1986, Angelescu & Prensky 1987, Ubal *et al.* 1987c, Olivieri & Christiansen 1987, Norbis 1998, 1999a). The growth and mortality of hawkfish and hake were studied by Norbis (1992) and Lorenzo (1999a, 1999b). Nión *et al.* (1986) described a multispecific nursery ground over the inner shelf, and an important hake nursery area on the Uruguayan continental shelf in autumn and spring was found by Rey *et al.* (1996), Norbis *et al.* (1999), Mantero & Errea (1999) and Errea *et al.* (1999); juveniles of *C. bergi* were also detected here (Galli & Norbis, 1992). The relationships between hake nurseries and oceanic fronts were analysed by Norbis & Severov (1999) and Severov (1999).

The anchovy (*Engraulis anchoita*), the horse mackerel (*Trachurus lathami*), the mackerel (*Scomber japonicus*), and the blue fish (*Pomatomus saltatrix*) are the most abundant pelagic species (Brandhorst *et al.* 1971a, 1971b, 1971c, Ehrhardt *et al.* 1977b, Nión & Ríos 1991, Alheit *et al.* 1991). Other species such as *Thunnus alalunga*, *Thunnus albacares*, *Thunnus obesus*, and *Xiphias gladius* are also important components of the pelagic oceanic system (Ríos *et al.* 1986, Nión & Ríos 1991, Marín *et al.* 1998, 2000). An analysis of the principal groups of demersal fishes by latitude, depth, and bottom type was presented by Abella *et al.* (1979); this included 80 genera and more than 140 species. Various authors (Menni & Gosztanyi 1982, Ishino *et al.* 1983, Angelescu & Prensky 1987, Prensky & Sánchez 1988, Norbis 1993, 1999b, Díaz de Astarloa *et al.* 1999, Menni & Stehmann 2000) addressed different aspects of the demersal fish's assemblages over the continental shelf, mainly related to composition, abundance, diversity, and how these depended upon latitude, depth, temperature, and salinity. Stomach content analyses for coastal species are scarce (Mora & Pintos 1980, Puig 1986, Leta 1987, Masello *et al.* 2001). Possible trophic relationships in the coastal system were discussed by Olivier *et al.* (1968), while some were demonstrated for the hake foodweb (principally involving zooplankton, anchovy, and squid) (Ubal, 1986; Angelescu & Prensky, 1987 and Galli, 1999). An analysis of the feeding of elasmobranch fish was performed by Paesch (2000).

Marine mammal species that live in or visit the area include *Arctocephalus australis*, *Otaria byronia*, *Pontoporia blainvillei*, *Tursiops truncatus*, and *Orcinus orca* among the former, and *Arctocephalus tropicalis*, *Mirounga leonina*, *Balaenoptera musculus*, *B. physalus*, *B. borealis*, *Eubalaena australis*, and *Megaptera novaengliae* among the latter (Ponce de León 1999). Research has focused mainly on sea-lion and fur seal populations (*O. byronia* and *A. australis*), and provided the basis for sustainable exploitation for many decades (Vaz Ferreira 1965, 1972, 1975a, b); there is now information regarding their ethology, growth, population dynamics, feeding, and interactions with artisanal fisheries (Vaz Ferreira 1987, Batallés *et al.* 1990, Lima & Páez 1995, 1997, Lima 1998, Szteren 1999, Ponce de León *et al.* 2000, Szteren & Páez 2002). Attention was also paid to the accidental capture of the Río de la Plata dolphin (*P.*

blainvillei), an endemic species of the RdLP and neighboring areas (ca. 18°30'-42°30'S), for which systematic records since the 1970s are available (Praderi *et al.* 1989, Little *et al.* 1997). Furthermore, recent examinations of genetic variability in the dolphins suggest the existence of a Río de la Plata-Río Grande population different from that further north (Rio de Janeiro, Brazil), and south (Claromecó, Argentina) (Lázaro 2001).

BENTHOS

Sandy beaches

Sandy beaches dominate ocean and estuarine shorelines of the 670 km Uruguayan coast (UNESCO 1980). Currently available information is mainly for macroinfauna, both at the community and population levels, particularly on exposed ocean beaches. However, data are particularly scarce or absent for plankton, meiofauna, vagile megabenthos, and nekton of the surf zone, as well as for birds and subterrestrial fauna of the sand dunes.

Communities: Investigations have focused on the description of the structure, seasonal dynamics, and patterns of distribution of macroinfauna at spatial scales ranging from macro (km) to meso (individual beaches). Escofet *et al.* (1979) provided general macroscale features of macroinfauna communities for sandy beaches of the Southwestern Atlantic coast from 29° to 43° S. Scarabino *et al.* (1974, 1975) documented general bionomic patterns and spatial variations of the macroinfauna in the upper littoral levels of the sandy beaches of Montevideo. Following the same approach, details about intertidal (Baccino 1984, Demichelli 1984) and sub-tidal (Demichelli 1984, 1985a) populations were provided for the macroinfauna inhabiting a semi-exposed sandy beach. Demichelli (1985b) also characterized the sub-tidal community structure of an exposed Atlantic sandy beach. Quantitative macroscale patterns were formerly determined through a snapshot study covering a complete range of dissipative-reflective categories of Atlantic sandy beaches (Defeo *et al.* 1992a).

Initial studies directed towards distinguishing faunal zonation across beaches were qualitative in nature (Scarabino *et al.* 1974, 1975, Demichelli 1984, 1985a, b, Baccino 1984) or based on a very short

time scale (one sampling date) (Defeo *et al.* 1992a). More recent work has adopted a quantitative approach with monthly samplings for up to a year on exposed beaches of the Atlantic coast of Uruguay. These showed significant spatial variability in zonation with aperiodic and seasonal components (Brazeiro & Defeo 1996, Giménez & Yannicelli 1997).

Alongshore variations in community structure were examined mainly to assess the spatial and temporal effects of a freshwater discharge on the macroinfaunal community and its habitat in a sandy beach of Uruguay (Lercari & Defeo 2002).

Populations: Studies at the population level were targeted at answering specific questions, notably those related to medium/long-term variations in abundance, responses of the species to beach morphodynamics, dynamic variations in abundance in the across and alongshore axes, responses of the species to disturbances (e.g. harvesting and freshwater discharge), population dynamics (e.g. growth, mortality, and recruitment), and assessment of the relative contribution of biotic and abiotic factors regulating populations.

Abundance, demography, and population dynamics were the main factors studied in the yellow clam, *Mesodesma mactroides* (Defeo 1993, Seijo & Defeo 1994, Brazeiro & Defeo 1999). Data from an 8 year study included an experimental manipulation of the fishing effort based on the closure of the clam fishery for 32 consecutive months (Defeo 1996a, 1998, Lima *et al.* 2000, Castilla & Defeo 2001). A long-term analysis of the structure of a population of another sandy beach bivalve, the wedge clam *Donax hanleyanus*, was carried out by Defeo & de Alava (1995) and Seijo *et al.* (1994).

Growth, mortality, and recruitment parameters were estimated for different sandy beach populations using a wide range of frameworks in order to test specific hypotheses (Defeo 1985b, de Alava & Defeo 1991, Arreguin *et al.* 1991, Defeo *et al.* 1988, 1992b, c, 2001, 2002, Brazeiro & Defeo 1999, Gómez & Defeo 1999). Reproductive biology studies (Masello & Defeo 1986) were useful complements to those of population dynamics (Defeo *et al.* 1992b).

Alongshore gradients were quantified in sandy beach populations of Uruguay (Defeo 1985a, Defeo *et al.* 1986, 1988, de Alava and Defeo 1991, Riestra *et al.* 1996, Giménez & Yannicelli 1997, 2000). Species-

specific behavioral responses to swash climate, manifested in swimming ability, burying, and orientation to directional flows, were addressed by Yannicelli *et al.* (2001, 2002). The across-shore population structure and abundance of sandy beach macroinfauna was recently derived from design-based (stratified random sampling) and model-based (geostatistics, kriging) approaches (Defeo & Rueda 2002), and the effect of morphodynamics on the life history traits of such populations was investigated by Defeo *et al.* (1992a, 2001, 2002), McLachlan *et al.* (1995), and Gómez & Defeo (1999). The role of sediment characteristics and potential interactions in determining the abundance and distribution patterns of the cirrolanid isopods *Excirolana armata* and *Excirolana brasiliensis* in sandy beaches of Uruguay have also been examined (Defeo *et al.*, 1997).

In addition to natural biotic and abiotic factors, various forms of human-induced perturbations affect the nearshore, benthic environment in exposed sandy beaches, notably fishing, building, and pollution coming from discharges from wide plain basins used for agriculture and cattle rearing, and subjected to agro-chemicals (Defeo & Lercari 2000, Brazeiro 2000, Lubchenco *et al.* 1995).

Species supporting current fishing activities (*Mesodesma mactroides*) or likely to do so in the future (*Donax hanleyanus*, *Emerita brasiliensis*); have been studied in Uruguayan beaches (Defeo 2002). These have intertidal distributions but most are centered in the swash zone or shallow sub-tidal area. Recreational fisheries on sandy coasts have been shown to be extremely difficult to manage since the numbers of fishermen cannot usually be controlled and measures to prevent over-exploitation are based on size and catch limitations and seasonal/area restrictions (Defeo 1987, 1989a, b, Defeo *et al.* 1991a, 1993, Seijo & Defeo 1994, Seijo *et al.* 1994). A successful example of improving the management of coastal shellfisheries through natural repopulation, rotation of areas, and the allocation of property rights (individual quotas) was documented for the small-scale fishery of *M. mactroides* (Defeo 1993, 2000). Experimental manipulation of the yellow clam fishery was used to evaluate changes in the overall abundance of harvested (*M. mactroides*) and unharvested (*D. hanleyanus*) bivalves, as well as in the processes regulating their population dynamics (Defeo 1996a, b, 1998; reviewed in McLachlan *et al.* 1996 and Castilla & Defeo 2001).

The potential effects of freshwater discharge from a man-made canal on the wedge clam *D. hanleyanus* were analyzed as functions of time and space (along-shore variation) (Defeo & de Alava 1995, 2002). Similar studies were carried out on sandy beach gastropods (Defeo *et al.* 1996) and the mole crab *Emerita brasiliensis* (Lercari & Defeo 1999, Defeo & Lercari 2000). Further work demonstrated the spatial effects of freshwater canal discharge on the habitat and resident macrobenthos of a Uruguayan exposed sandy beach through a combined analysis of communities, populations, and the surrounding habitat (Lercari & Defeo 2002). Overall, it must be concluded, future research on sandy beach populations should include human activities as important factors affecting long-term trends.

Marine rocky shores

Rocky habitats occupy a very narrow portion of the Uruguayan coast. Basically, the littoral fringe is dominated by extensive sandy arcs delimited by rocky headlands or freshwater discharges. However, these rocky ecosystems sustain a rich biological diversity, and important artisanal fisheries (e.g. blue mussels).

The biodiversity of rocky intertidal and shallow sub-tidal habitats is comparatively well known, with important differences between taxonomic groups (Masello & Menafrá 1996, Brazeiro 2000). Molluscs, Decapoda (i.e. Amaro 1965, Scarabino *et al.* 1975, Maytía & Scarabino 1979, Batallés 1983, Riestra *et al.* 1992, Riestra 1999) and algae (Coll 1979, Méndez 1982) are the best described taxonomic groups, while others like amphipods, isopods and polychaetes, are poorly known.

The geographic and local distributions (zonation patterns) of the biota have been qualitatively described (Scarabino *et al.* 1975, Maytía & Scarabino 1979, Neirotti 1981, Batallés *et al.* 1985). Community structure, including species richness and composition, is only well known at specific localities like Punta del Este, where relatively long term studies have been carried out (Riestra *et al.* 1992, Riestra & Defeo 1994, Riestra 1999). On a larger geographical scale, the salinity gradient produced by the interaction between the RdIP and the Atlantic Ocean has been suggested as the main factor determining the variations in the distributional and compositional patterns (Maytía & Scarabino 1979).

In accordance with this hypothesis, a massive mortality of marine organisms on the Atlantic coast was ascribed to a fresh water intrusion from the RdIP (Riestra *et al.* 1997). On a more local scale, the effect of harvesting the blue mussel *Mytilus edulis platensis* on the macrobenthos was the only ecological factor studied in relation to community organization (Riestra *et al.* 1992, Riestra & Defeo 1994, Riestra 1999).

Population patterns and processes such as abundance, growth, recruitment, and mortality have been studied only in the exploited population of the blue mussel (*Mytilus edulis platensis*) of Punta del Este (Abdala 1981, Berocay 1983, Batallés & García 1984, Riestra & Defeo 1994). The characteristics of this artisanal fishery have been very well documented (Arena *et al.* 1989a, b, Niggemeyer & Masello 1992).

Basic information about an invader species, the bivalve *Limnoperna fortunei*, was reported by Scarabino & Verde (1994). This exotic mussel is native to China and Southeast Asia and has been spreading in the RdIP since 1991, populating various types of hard substrates in freshwater and euryhaline zones.

Estuarine habitats

Estuarine benthic habitats are comprised of the RdIP estuarine system and associated subestuaries of the outer RdIP (e.g. the rivers Santa Lucía and Solís Grande) and a group of small estuaries located at river mouths and in coastal lagoons on the Atlantic coast (e.g. the Maldonado and Valizas rivers and Rocha and Castillos lagoons).

Information about species composition comes from quantitative sampling as well as qualitative observations and collections in several sites along the Uruguayan coast. These data are mainly for macrofauna and show that the benthic habitats are, in general, dominated by only a few species of crustaceans, molluscs, and polychaetes.

Information about species composition and patterns of distribution of the macroinfauna of RdIP were reviewed by Massello & Menafrá (1997) and Mianzan *et al.* (2000). On the Uruguayan coastline, only a few sites have been studied with respect to species composition, patterns of distribution, and community structure, namely Montevideo Bay (Danulat *et al.* 2002), the Solís Grande subestuary,

(Bier 1985, Muñoz & Venturini 2001), Rocha lagoon and the Valizas stream (Nión 1979, Corbellini 1983, Cardezo 1989, Pintos *et al.* 1991, Jorcín 1993, 1999). Seasonal variations in macroinfaunal abundance in the Rocha lagoon and the Valizas stream were also studied by the previously named authors. An experimental study focused on the effects of eutrophication on the abundance of the macrobenthos (Arocena 2000), whereas another examined the benthic fauna in a highly contaminated area (Danulat *et al.* 2002).

Studies of the life history and ecophysiology of the estuarine macrobenthos made either in Uruguay or by Uruguayan scientists working elsewhere concerned the crab *Chasmagnathus granulata* and examined survival, growth, and osmoregulation in embryos (Giménez & Anger 2001), adults (Holcman-Spector *et al.* 1973, Mañé-Garzón *et al.* 1974, Gnasso *et al.* 1978), and larvae (Giménez 2000, 2002, Charmantier *et al.* 2002).

The continental shelf benthic ecosystem

Taxonomic and faunal knowledge is limited and scattered for most groups of macrobenthos. Biogeographically, the fauna that inhabit the continental shelf ecosystem of Uruguay integrate components of the Magellanic, Argentinean and Indean Provinces (López 1964, Scarabino 1977, Menni & Stehmann 2000). The few studies conducted at community level related to soft bottoms (Milstein *et al.* 1976, Cachés 1980, Masello *et al.* 1996, Venturini *et al.* 1999) or were part of an investigation of the feeding habits of commercially exploited stocks such as the croaker, *Micropogonias furnieri* (Puig 1986). Ecological studies of particular invertebrate groups are also few and restricted to molluscs (Olivier & Scarabino 1972, Layerle & Scarabino 1984), polychaetes (Elgue & Faget 1986), and ophiuroids (Lucchi 1985). Information about benthic fish is, on the other hand, more abundant (Abella *et al.* 1979, Arena *et al.* 1993, Díaz de Astarloa *et al.* 1999, Paesch 1999, Fabiano *et al.* 2000a, Spinetti 2000, Paesch 2000, Meneses 1999, Menni & Stehmann 2000). Research and commercial surveys of several megabenthic invertebrates provided preliminary information about the targeted species and their associated fauna. These species include the gastropods *Zidona dufresnei* and *Pachycymbiola brasiliana* (Fabiano *et al.* 2000b, Riestra *et al.* 2000), the blue

mussel *Mytilus edulis* (Juanicó & Rodríguez 1976, Amaro 1979), and the Patagonian scallop *Zygochlamys patagonica* (Defeo & Brazeiro 1994, Defeo & Gutiérrez 2000, Riestra & Barea 2000, Riestra 2000).

The slope and abyssal plain

Here too, taxonomic and faunal data are scarce and restricted to those that resulted from 3 comprehensive surveys by research vessels – the Challenger (2 stations), the Atlantis II (macrobenthos of southern zone), and the Walther Herwig (megabenthos); all samples were from soft bottoms. The level of endemism reported for an important macrozoobenthic group (the Bivalvia Protobranchia) in this region is the highest among the deep-sea basins of the Atlantic Ocean (Allen & Sanders 1997). Biogeographic affinities deduced from this group are enigmatic, with possible relations with the Angola Basin and southern Pacific (Allen & Sanders 1997). Autoecological and biological knowledge exists only for a very few megabenthic species: the red crab *Chaceon notialis* (Defeo *et al.* 1989, 1991b, Defeo & Masello 2000a, 2000b), the octopus *Vosseledone charrua* (Leta 1992), the starfish *Bathybiaster herwigii* (Scarabino 1983), some gastropods (Olivier & Scarabino 1972), and skates (Menni & Stehmann 2000).

THE UNKNOWN

PLANKTON

Studies of plankton systematics and distribution in coastal areas shallower than 10m have contributed disproportionately to the investigations. Physical processes and patterns of biological production in the pelagic zone are central to the understanding of the biogeography of marine life (Longhurst 1998, Woodd-Walker *et al.* 2002).

Thus, a functional approach to the study of these processes is strongly required to complement existing knowledge in this area. This will require multidisciplinary studies ranging from research on individual physiological responses to large-scale programs directed towards discerning physical-biological coupling processes, and should include laboratory, field, and modeling efforts.

Present understanding of the zonation patterns along

environmental gradients within the RdIP (i.e. salinity, turbidity) is very fragmentary. Efforts are needed to investigate the forcing factors behind the patterns involving the identification of dominant or key species (*sensu* Verity & Smetacek 1996), as well as the study of their life history traits, population dynamics, and responses to the variable environment. The characterisation of salinity tolerance ranges and how feeding and production vary with changes in environmental conditions are also important. Special attention must be given to frontal zones (within the RdIP as well as over the shelf), since they may represent zooplankton “hot spots” (*sensu* Paffenhöfer 2001).

Seasonal patterns of phytoplankton and zooplankton biomass and production are poorly known, as is how these variables are affected by environmental variability on different time-scales (e.g. coastal eutrophication and long-term increments in RdIP outflow; Nagy *et al.* 1997). There is a lack of time series of biological variables required to explore long-term trends and low frequency cycles related to environmental variability. An exception is a monitoring program focused on potentially toxic dinoflagellates being carried out at coastal sites (Méndez *et al.* 1997); it would be profitable to enhance this work by incorporating simple protocols for measuring phytoplankton and zooplankton biomass. There is also a strong need to build up a thorough picture of primary production and its temporal variability over the whole area, as well as of the factors which regulate production—light, nutrients, and grazing—which are likely to vary between the seasons and different areas (e.g. light limitation in the highly turbid waters of the RdIP vs. nutrient limitation over the shelf).

There is no information regarding trophodynamics within the plankton assemblage and the fate of locally produced organic matter. No estimations of ingestion rates have been made for any zooplankton group and the relative contribution of the small fractions (i.e. zooplankton <200µm) to the total grazing pressure on phytoplankton has not been documented. Protozoan plankton (ciliates and flagellates), which are well known to reach high densities in estuarine areas (Smetacek 1981, Gifford & Dagg 1988, Day *et al.* 1989, Lalli & Parsons 1997) may play a crucial role in the cycling of organic matter and making it available to the grazer food chain. Potentially dominant mesoplankton grazers in the

RdIP (e.g. *Acartia tonsa*) are especially able to switch from herbivory to carnivory (Kiorboe & Sáiz 1995, Saiz & Kiorboe 1995). Given the high availability of particulate organic matter, it would be relevant to estimate the significance of the algal diet at different seasons and areas in order to assess the coupling between primary and secondary production.

Future research should incorporate modelling efforts to condense empirical results and guide further observations and experimentation. In this respect, models on physical-biological coupling would be particularly interesting, considering that several physical models for the RdIP have been proposed or are under development.

NEKTON

Studies of the littoral coastal system are scarce and those existing have not adopted an integrated ecosystem approach. Fish and their role in the surf-zone of sandy beaches are largely unknown. There is a lack of information on the taxonomy and distribution of clupeids, myctophids, and other groups. Data on feeding habits and trophic ecology are scarce and mainly limited to studies of commercially important species. Life-cycles and population dynamics of the majority of groups are incompletely known. The relationships between spawning types, spawning areas, environmental variability, and the structure of the spawning stock during the reproductive period have also received little attention. Information regarding the growth of juvenile fish in relation to environmental variability and feeding availability is limited. Also, the effect of fisheries on diversity and community structure is largely unknown.

BENTHOS

Sandy beaches

Information is particularly scarce and sometimes absent for the plankton, meiofauna, vagile megabenthos, and nekton of the surf zone, as well as for birds and the sub-terrestrial fauna inhabiting sand dunes. In this context, an ecosystem approach is needed for modeling interrelations between different components of food webs as well as the nature and extent of the networks of interactions between species. Other processes and mechanisms (e.g. predation, commensalism, parasitism, and mutualism) that affect the structure

and functioning of sandy beach populations and communities are still unknown. The sub-tidal fringe has been little explored, particularly with regard to basic knowledge about systematics and the general characteristics of the fauna at the community and population levels.

Long-term, large-scale monitoring of the structure and dynamics of sandy beach macroinfauna, as well as the concurrent effect of the estuarine gradient (RdIP) and morphodynamics on the fauna inhabiting these systems needs to be initiated. Knowledge of biodiversity gradients is fragmentary, particularly for certain taxonomic groups (e.g., components of the meiofauna and polychaetes) in fields such as taxonomy and systematics, as well as the inherent characteristics of their life histories. Furthermore, the macroecology of population dynamics and biogeographic patterns in life histories have not been adequately assessed in sandy beach ecology (Defeo & Cardoso 2002).

Little is known about the dispersive abilities of meroplanktonic larval phases of sandy beach macrofauna and the mechanisms influencing larval distribution are poorly understood (Defeo 1996b). Research should focus on planktonic stages and the role of near-shore hydrodynamics in settlement processes. This could determine the degree to which population dynamics is related to the arrival rates of larvae rather than to post-settlement processes. Physical oceanographic information related to larval dispersal would be of importance in this context.

Recent results obtained by Uruguayan scientists support the view that beach morphodynamics may not be the primary factor affecting the life history traits of the macrofauna. The fact that unsimilar responses of populations could also result from locally adapted genotypes or a combination of plastic and genetic responses should be addressed through genetic studies on a macroscale.

Laboratory evidence is not extensive enough to reflect the variety of environmental regimes found at particular sites and their effects on benthic fauna. The physiological factors controlling species distribution and abundance need to be addressed together with ethological studies in order to evaluate the relative contributions of the factors influencing sandy beach fauna.

The exploitation of beach clams is often restricted by their accumulation of toxins such as those associated with certain algal blooms (Defeo &

Scarabino 1990); these can cause mass mortalities of clams and/or render them unsafe for human consumption. This limits the potential utilization of many stocks and creates the need for careful monitoring and management. As human impacts on coastal waters continue, blooms of toxin-producing phytoplankton could increasingly affect filter feeders. This should be a focus for future studies.

Despite their potential importance, very little is known about the consequences of natural or human-induced disturbances on the structure and dynamics of sandy beach populations and communities. Different approaches are needed to perform well-designed experimental and field studies directed towards critically assessing environmental impacts in these fragile ecosystems. This research should be complemented by laboratory (microcosm) experiments directed to determine the ecophysiological effects of pollutants and responses to abiotic factors.

Spatial and temporal variations in growth, mortality, and recruitment rates in sandy beach populations may be partially related to density-dependent processes (Defeo 1993, 1998). Future work should emphasize scale-dependent experimental manipulations of abundance. Moreover, the spatially discrete analysis of sandy beach populations, their surrounding environment and, eventually, the fishery will be a useful means for monitoring changes in abundance and structure, as well as in population dynamics parameters and environmental variables. An integrated approach to develop a comprehensive management scheme could be of the utmost importance for impact assessment studies (Defeo *et al.* 1991, 1993, Seijo & Defeo 1994, Lercari & Defeo 1999).

Marine rocky shores

Descriptions of the biodiversity of rocky coastal habitats are scarce and completing our understanding of this biota will require great effort for some taxonomic groups, especially those inhabiting the mussels domain such as the Amphipoda, Isopoda, Polychaeta, Cnidaria, Turbellaria, Nemertea, and Nematoda.

The description of community patterns is in its early stages. Quantitative research on the relationship between different community traits (species richness and composition, abundance distribution) and environmental factors (exposure, habitat complexity, energy input, seascape configuration, pollution) is needed to understand community structure. The dynamic aspects

of these communities, such as extinction and colonization rates, are unknown. The processes and mechanisms underlying the community structure are also far from being understood. Natural and field experiments would provide useful information. At the population level, only the demography of the blue mussel is relatively well known. There is no similar information for other species on rocky shores. Ecosystem studies of food webs, productivity, and the fluxes of particulate matter are nonexistent. Information useful for conservation purposes like conservation status, the level of endemism, and the rarity of species, or the localization of "hot-spots" in terms of high species richness or degree of endemism, are not available for Uruguayan rocky shores.

Estuarine habitats

Taxonomic and faunal data for benthic meiofauna and microfauna are similarly meagre. Again, basic knowledge such as patterns of distribution and community structure on a macroscale as well as temporal variability in abundance at most estuarine sites is not available. A research program that combines sampling and experimental approaches needs to be initiated in order to understand how the estuarine communities of the Uruguayan coast are structured and discover the similarities with and/or differences from other populations in the region; this should include an evaluation of the role of presettlement processes (e.g. larval transport and survival in the field) and postsettlement factors (predation, competition, physical stress) which affect species distribution. Similar requirements hold for ecosystem studies since these species are the prey of several fish; this could influence the transfer of nutrients and organic matter between the bottom and the water column.

The continental shelf benthic ecosystem

Taxonomic and faunal knowledge is inadequate for most groups of the macrofauna and there have been no studies of the meiobenthos or microbiology. Comprehensive research at the community and population levels is lacking, particularly for rocky bottoms. Community approaches have seldom been used for soft and, especially, hard bottoms, and biological, ecological, and biogeographical data are unknown for most species. The effect of fishing on the habitat and fauna inhabiting benthic ecosystems of the continental shelf remains to be examined.

TABLE I. Summary of the degree of knowledge reached for the different groups and habitats in Uruguayan waters, and recommendations for future research. 1=unknown or very poorly known; 2= insufficiently known; 3= relatively well known. ES= estuaries, RS= rocky shores, WA= whole area, SH= shelf, SB= shelf-break and abyssal plain.

TABLA I. Resumen del grado de conocimiento alcanzado para los diferentes grupos y ambientes de aguas uruguayas, y recomendaciones para próximas investigaciones. 1= desconocido o muy poco conocido; 2= parcialmente conocido; 3= relativamente bien conocido. ES= estuaries, RS= rocky shores, WA= área entera, SH= plataforma, SB= shelf-break and abyssal plain.

		Littoral		Shelf	Shelf-break & deep ocean	Recommendations
		Beach	Coast<10m & estuaries			
Plankton	Taxonomy	1	2	2	1-2	Taxonomy, distribution & processes over the WA
	Patterns	1	2	2	1-2	
	Processes	1	1	1	1	
Benthos	Taxonomy	3	1-2	1-2	1	Micro-meiofauna (WA), macrofauna (ES, SH & SB) WA WA
	Patterns	3	1-2	1	1	
	Processes	2	1	1	1	
Nekton	Taxonomy	1	3	2	2	For selected groups Interactions between components & anthropic effects Population dynamics, environmental effects & trophodynamics
	Patterns	1	2	2	1	
	Processes	1	2	2	1	

The slope and abyssal plain

Biotic aspects of the slope and abyssal plain are scarcely known, particularly for the northern zone of Uruguayan waters and the rocky bottoms. There have been no studies of the meiobenthos or microbiology, or of the macro- and megabenthos. Biogeographical issues and the specific characteristics of the life history traits of most species are unknown. A general biogeographic scheme has not been developed.

CONCLUSION

Table I summarises the known and the unknown aspects of marine life in Uruguayan waters. Future

research will need to cover a wide spectrum of subjects and the proposals here may appear as rather ambitious. They will certainly take several years to consolidate. Research topics common to different groups include taxonomy, analysis of community structure on the macroscale and its temporal variability in relation to environmental gradients, population dynamics, trophodynamics, and the effects of human intervention on ecosystems. Issues such as meroplankton ecology and the fate of pelagic production may serve as links between benthic and planktonic studies; this is also the case in trophodynamical aspects of the early life stages of fish which involve the transfer of energy and matter between plankton and nekton. Finally, the incorporation of experimental and modeling approaches are recognized as important in future investigations.

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