

TESIS DE DOCTORADO –PEDECIBA

Eutrofización de las lagunas costeras de Uruguay: impacto y optimización de los usos del suelo



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RESUMEN

Las lagunas costeras son ecosistemas someros que se conectan con el mar de manera permanente o intermitente e intercambian masas de agua dulce y salada. Son sistemas complejos debido a la conexión con el mar, el gradiente salino y el intercambio de organismos y sustentan servicios ecosistémicos que son intensamente utilizados por la población, haciendo más complejo su funcionamiento. Las lagunas costeras de Uruguay (L. José Ignacio, Garzón, de Rocha y de Castillos) se conectan periódicamente con el Océano Atlántico a través de la apertura de un canal en la barra arenosa. La pequeña L. del Diario se conectaba con el Río de la Plata hasta la década de 1950 cuando la construcción de una ruta costanera interrumpió la conexión natural. El uso predominante del suelo en la cuenca de estas lagunas es la ganadería extensiva sobre praderas naturales y recientemente se incrementó la forestación con especies exóticas y la agricultura y en L. del Diario la urbanización. La existencia de floraciones de cianobacterias, proliferaciones de plantas y aumento de los valores máximos de nutrientes en estas lagunas indican que existe un proceso de eutrofización posiblemente debido a un cambio en los usos del suelo. El objetivo de este trabajo es evaluar la influencia del uso del suelo en las cuencas de cinco lagunas costeras de Uruguay en los indicadores de eutrofización, determinar el efecto de la conexión con el mar en dichos indicadores y la configuración óptima de usos que minimice el proceso de eutrofización y la pérdida de biodiversidad. Para esto se adoptó una estrategia de estudio a diferentes escalas espaciales y temporales. El cambio en el uso del suelo en las cuencas se determinó mediante análisis de imágenes satelitales, abarcando 30 años de estudio. La carga total de nutrientes exportada desde la cuenca se estimó multiplicando la superficie de los usos del suelo identificados en cada imagen satelital por coeficientes de exportación de nutrientes específicos. Se realizó un monitoreo estacional de dos años de duración de indicadores de eutrofización (nitrógeno y fósforo disueltos y total del agua y total del sedimento, clorofila de fitoplancton y de fitobentos y biomasa de plantas acuáticas sumergidas), en las cinco lagunas estudiadas y se relacionó el valor de dichos indicadores con la superficie de los usos del suelo actuales mediante regresiones simples. Para determinar si la abundancia de plantas sumergidas y concentración de nutrientes se incrementó en el tiempo se analizó mediante modelos lineales generalizados una serie de datos de seis años en L. de Rocha y se analizó el registro plínico de sedimentos recientes de las cuatro lagunas costeras con conexión al mar. Por último, se realizó una modelación multi-atributo y multi-objetivo para analizar la configuración de usos del suelo en la cuenca de las lagunas con conexión al mar que minimice el proceso de eutrofización y la pérdida de biodiversidad a la vez que permita el desarrollo de actividades agropecuarias y turísticas. Se observó un aumento de la forestación, siembras en cobertura y praderas artificiales en las cuencas estudiadas, aumentando moderadamente la exportación de nutrientes desde las cuencas. Este cambio fue muy marcado en L. del Diario debido al aumento de la población humana. Los indicadores de eutrofización mostraron una tendencia de aumento con la superficie de agricultura (para el fósforo total) y la carga de fósforo total exportada desde las cuencas y una clara disminución con la superficie de bosque nativo. No se encontraron efectos de la forestación. Los mecanismos de filtración del agua de escorrentía proveniente desde la cuenca que ocurren en el bosque y vegetación riparia explicarían la relación observada. Los indicadores de eutrofización disminuyeron con la salinidad, debido a la descarga de agua dulce al mar y a la dilución provocada por intrusiones marinas. La interrupción de la conexión con el mar de la L. del Diario sumado al incremento de la población humana explican el severo proceso de eutrofización observado. La modelación multi-criterio permitió identificar zonas homogéneas de aptitud de uso del suelo para la forestación, agricultura, conservación, turismo y ganadería. Se observó que los usos más intensivos y menos compatibles con el resto de los usos son los que presentan mayor potencial de expansión. La interferencia actual entre usos antagónicos (la realización de uno excluye a otros usos) es baja (menor al 5%) de las cuencas pero si todos los usos se expanden a sus territorios aptos puede aumentar al 23%, indicando que los conflictos entre usuarios pueden aumentar considerablemente. La optimización lineal permitió seleccionar los usos que deberían ser des-estimulados en las zonas de aptitud homogénea de manera de evitar conflictos y maximizar la aptitud total del sistema.

ABSTRACT

Coastal lagoons are shallow ecosystems that are permanently or periodically connected to the sea, exchanging freshwater and marine water. These lagoons are complex ecosystems due to the connection with the sea, the salinity gradient and the organisms exchange with the sea which sustains important ecosystem services that benefits local communities. The coastal lagoons of Uruguay (L. José Ignacio, Garzón, Rocha and Castillos) periodically connect with the Atlantic Ocean through the opening of a channel in the sandbar. The natural connection of the small L. del Diario with the Río del la Plata was interrupted during 1950's when a coastal road was constructed. The dominant land use in the basin of these coastal lagoons is livestock ranching on natural grassland but recently afforestation and agriculture increased, while in L. del Diario the main change was urbanization increase. The presence of cyanobacteria blooms, submerged aquatic plants proliferations and nutrients increase in these systems indicate an eutrophication process possibly driven by land use changes. The aim of this study was to evaluate the influence of land uses in the eutrophication indicators of five coastal lagoons of Uruguay, to determine the effect of the connection to the sea in these indicators and to obtain the optimal configuration of land uses that minimizes the eutrophication process and biodiversity loss. We adopted a multi-scalar approximation in time and space. The land use change in the catchment area was determined by the analysis of satellite images spanning 30 years of study. The total nutrient load exported from the catchment area was estimated by multiplying the area of each land use by specific nutrient export coefficients. Seasonal monitoring of eutrophication indicators (dissolved and total nitrogen and phosphorus, total nitrogen and phosphorus in the sediments, chlorophyll *a* of phytoplankton and phytobenthos and biomass of submerged aquatic plants) was conducted during two years in the five coastal lagoons. The effect of land uses on eutrophication indicators was determined with simple regression analyses. To determine if the abundance of submerged plants and nutrients concentration increased over time we analyzed a six years data base with generalized linear models in L. Rocha. We also analyzed the pollen record in recent sediments of the four coastal lagoons which still connects to the ocean. Finally, we conducted a multi-attribute and multi-objective modeling to analyze the configuration of land uses in the catchment area of the coastal lagoons that still connects to the ocean, to minimize the process of eutrophication and biodiversity loss while allowing the development of afforestation, agriculture, livestock ranching and tourism. An increase of afforestation, over sowing and artificial prairies was observed in the catchment area of the coastal lagoons of Uruguay, followed by a moderate increase of the nutrient loads. This change was most marked in L. del Diario due to the increase in human population. Eutrophication indicators showed an increasing trend with the surface of agriculture (for total phosphorus) and with the total phosphorus load, while a clear decrease with the surface of native forest. We observed no effects of afforestation. Filtration mechanisms of runoff promoted by the riparian vegetation may explain the effects of native forests. Eutrophication indicators decreased with salinity due to freshwater discharge to the sea and the dilution caused by seawater intrusion. The interruption of the connection to with sea in L. del Diario and the human population growth explains the severe eutrophication process in this lagoon. The multi-criteria spatial modeling identified homogeneous areas of land use suitability for afforestation, agriculture, conservation, tourism and livestock ranching. The most intensive and competitive lands uses are those with the greatest potential for expansion. The actual interference between conflicting land uses (when the allocation of a specific land use exclude an other land use) is low (less than 5%) but if all uses expands to their suitable territories conflicts can increase up to 23%. The linear optimization procedure allowed selecting the land uses that should be des-stimulated from suitability homogeneous areas in order to avoid conflicts and maximize the total suitability of the system.

RESUMEN EJECUTIVO

Uruguay presenta un sistema de lagunas costeras que se conectan periódicamente con el mar a través de la apertura de un canal en la barra arenosa ubicada en la costa. Esta dinámica de apertura intermitente determina el ingreso de masas de agua marina y el intercambio de organismos costeros, que ingresan a las lagunas a alimentarse y reproducirse. Son ecosistemas muy productivos y de alta biodiversidad de aves y presentan paisajes muy atractivos, por lo que sustentan pesquerías artesanales costeras y una creciente industria turística, además que se encuentran entre los sitios de mayor prioridad para ingresar al Sistema Nacional de Áreas Protegidas. Las lagunas que aún mantienen conexión con el Océano Atlántico son José Ignacio, Garzón, de Rocha y de Castillos, mientras que a la Laguna del Diario que se conectaba con el Río de la Plata, se le obstruyó dicha conexión en la década de 1950 con la construcción de la rambla. Acompañando la tendencia mundial de intensificación de los usos del suelo, Uruguay ha experimentado en la última década un incremento de las actividades agrícolas e incluso una transformación de la ganadería extensiva sobre pasturas naturales a formas más intensivas que requieren fertilización. Estas lagunas presentan indicios de un proceso de eutrofización, a excepción de Laguna del Diario donde dicho proceso está completamente instalado, indicado por un excesivo desarrollo de plantas sumergidas y elevada carga de nutrientes en el sedimento. Si bien el proceso de eutrofización en las lagunas que aún mantienen conexión al océano no ha alcanzado niveles críticos, y dado el alto valor turístico y de biodiversidad de estos sistemas, es oportuno plantear alternativas de ordenamiento ambiental que tiendan a minimizar este proceso y la pérdida de biodiversidad, en un contexto de incremento del desarrollo productivo y turístico de la zona. El objetivo general de la tesis es evaluar la influencia del uso del suelo en las cuencas de cinco lagunas costeras de Uruguay en los indicadores de eutrofización y determinar la configuración óptima de usos que minimice el proceso de eutrofización y la pérdida de biodiversidad.

El cambio del uso del suelo se determinó mediante el análisis de una serie de imágenes satelitales desde 1974 a 2005 y de los censos agropecuarios y de población. La carga de nutrientes exportada desde las cuencas a las lagunas se estimó mediante la aplicación de coeficientes de exportación de nutrientes a cada uso específico y se analizó la evolución de dicha carga en el tiempo. Se observó un cambio en el uso del suelo, que fue más intenso a partir de 1996, donde la forestación se implantó como una importante actividad económica, mientras que la agricultura se expandió. Si bien la población en la cuenca de las lagunas costeras no se ha incrementado significativamente desde 1984 a 2004, se observó el desarrollo de algunos balnearios o pequeños pueblos en las márgenes de las mismas. Contrariamente, en Laguna del Diario el incremento de la población fue elevado en la última década. Estos cambios implicaron en general un aumento moderado de la carga de nutrientes exportada hacia la laguna, excepto en Laguna del Diario donde el aumento fue importante. La carga de nutrientes por unidad de superficie fue máxima en Laguna del Diario, seguida de Laguna de Rocha, las dos cuencas más pobladas. Los usos del suelo que exportaron mayor cantidad de nutrientes fueron la ganadería extensiva debido a su gran superficie y la ocupación humana debido a sus elevados coeficientes de exportación.

En las cinco lagunas costeras estudiadas se realizó un monitoreo de indicadores de eutrofización en el agua (nutrientes totales y disueltos), en el sedimento (nutrientes totales) y de las comunidades de productores primarios más abundantes (abundancia de plantas sumergidas, fitoplancton y fitobentos), además de otras variables relevantes como salinidad (indicador de la conexión entre la laguna y el mar) y sólidos en suspensión, entre otros. El monitoreo fue estacional durante un año y medio (2005 y 2006). Se observó una alta variabilidad de todos los indicadores en el tiempo y en el espacio, pese a lo cual existió un gradiente claro de salinidad que aumentó con la cercanía al mar, e inverso a éste un incremento de los nutrientes y de la abundancia de productores primarios hacia la desembocadura de los tributarios en las zonas más límnicas.

Se analizó el efecto de los usos del suelo, de las características de las cuencas y de la salinidad en los indicadores de eutrofización de las lagunas, utilizando regresiones lineales y no lineales. La forestación no presentó efectos en los indicadores de eutrofización y la agricultura generó una tendencia a aumentar el fósforo total, a disminuir el nitrógeno total y disuelto y a aumentar significativamente los sólidos en suspensión. La carga de nutrientes exportada por las cuencas por unidad de superficie incrementó significativamente la abundancia de plantas sumergidas y el fósforo en el sedimento. El bosque nativo tuvo un efecto claro de disminución de los nutrientes que llegan a las lagunas y de la abundancia de los productores primarios (excepto el fitoplancton), mientras que por el contrario los humedales estarían aportando nutrientes a las lagunas. La salinidad en general disminuyó los valores de la mayoría de los indicadores de eutrofización. Según estos resultados, las cuencas están exportando cargas de nutrientes moderadas a las lagunas costeras a la vez que existen procesos que disminuyen los valores de los indicadores de eutrofización, como ser la retención de nutrientes en el bosque nativo y la descarga de agua al mar y posterior dilución con agua marina. Por el contrario, el estado hipereutrófico de la Laguna del Diario se explica por el incremento considerable de la carga de nutrientes exportada desde la cuenca debido al incremento poblacional, mientras que la supresión de la conexión al mar y la casi ausencia de bosque nativo en su cuenca indicarían la pérdida de los procesos que contrarrestan los aportes de nutrientes desde la cuenca, provocando una acumulación de nutrientes en el sedimento y proliferación de plantas sumergidas.

Se analizó información de seis años de abundancia de plantas sumergidas en la Laguna de Rocha, donde no se observó una tendencia al aumento de su abundancia sino una elevada fluctuación, con desarrollo de proliferaciones efímeras. Además, se determinó que la salinidad es el factor condicionante de la abundancia y riqueza de la comunidad y que si bien los efectos del aumento de los nutrientes no pueden ser descartados, los mismos no son claros.

Fue realizado un análisis del registro del polen del sedimento reciente de las lagunas que aún se conectan con el mar, donde se observó que las plantas sumergidas de las lagunas han estado presentes en las mismas al menos en los últimos 60-80 años, con importantes fluctuaciones en el tiempo, aunque no se observaron indicios de floraciones efímeras como la registrada en 2003 en Laguna de Rocha.

La aplicación de modelos multiatributo y multiobjetivo en la cuenca de las lagunas costeras de mayor tamaño reveló que los conflictos de uso del suelo actuales ocupan un 4.7% de la superficie de las cuencas, pero que los mismos podrían aumentar a un 20.3% de la cuenca si las actividades productivas como la forestación y la agricultura continúan expandiéndose en sus suelos aptos. Dicha expansión es esperable en el corto plazo, dada la tendencia de intensificación de los usos del suelo en la zona y la baja ocupación de los suelos aptos para dichos usos. Con esta metodología se obtuvo un mapa óptimo donde todos los usos son asignados a los suelos que presentan la mayor aptitud para desarrollar dicha actividad, evitando la coexistencia de usos que compiten por el mismo territorio. Estos resultados son útiles para orientar una política de ordenamiento territorial del país, complementando las formas *ad hoc* empleadas hasta el momento.

EXECUTIVE SUMMARY

The coastal zone of Uruguay is characterized by the presence of an important system of coastal lagoons. These large and shallow lagoons periodically connect with the ocean through breaches on their sand bars. This intermittent dynamic determines the entrance of seawater and coastal organisms into the lagoons to feed and reproduce. These coastal lagoons are highly productive and biodiversity rich ecosystems with outstanding landscapes which support both fisheries and a growing tourist industry. Additionally, these ecosystems are among the highest priority sites to integrate the National System of Protected Areas. The lagoons that still naturally connect with the Atlantic Ocean are José Ignacio, Garzón, Rocha and Castillos, while the natural connection of the Laguna del Diario with the Río de la Plata was modified by an artificial freshwater outlet when a coastal route was built in the 1950s. Following the global trend of land use intensification, over the last decade Uruguay has experienced an increase in agricultural activities and even a transformation of livestock ranching on natural pastures to more intensive practices requiring fertilization. These lagoons show evidence of an anthropogenic eutrophication process and in the Laguna del Diario this process is in an advanced phase, as indicated by excessive development of submerged plants and high nutrient content in the sediment. Therefore, there is a need to develop environmental management alternatives to minimize the eutrophication process and the loss of biodiversity, without compromising the economic development of the area. The overall objective of this thesis is to evaluate the influence of land uses in the catchment areas of five Uruguayan coastal lagoons on eutrophication indicators and to determine the optimal configuration of land uses that minimizes the process of eutrophication and biodiversity loss.

Land use changes were identified after analyzing a series of satellite images from 1974 to 2005 as well as the agricultural and population censuses. The nutrient load exported from the catchment areas into the lagoons was estimated by applying nutrient export coefficients for each specific land use, and the nutrient load evolution was also analyzed. Land use changes are evident and more intense since 1996, when afforestation was introduced as an important economic activity, while at the same time agriculture also expanded. The population in the coastal lagoons catchment has not increased significantly from 1985 to 2004, however several touristic resorts and small towns along the margins of the lagoons have developed. In contrast, in the Laguna del Diario catchment area the population increased drastically during the last decade. These changes generally involved a moderate increase in the nutrient load exported to the lagoons, except in the Laguna del Diario where the change was higher. Nutrient loading per unit area was highest in the Laguna del Diario, followed by the Laguna de Rocha, the two most populated catchment areas. The two land uses which exported the most nutrients were livestock ranching due to the large area utilized and human occupation due to the high export coefficients.

A seasonal monitoring of eutrophication indicators in the five coastal lagoons was conducted in 2005 and 2006. Eutrophication indicators in water (total and dissolved nutrients), in sediment (total nutrients) and the main communities of primary producers (abundance of submerged plants, phytoplankton and phytobenthos) were analyzed as well as other relevant limnological variables such as salinity (indicator of the connection between the lagoon and the ocean) and suspended solids, among others. In general in all lagoons, a high variability of all indicators over time and space was observed, and there was a clear salinity gradient. Salinity increased with proximity to the sea while at the other extreme of the gradient, at the mouth of the tributaries in the limnic zones, an increase of nutrients and the abundance of primary producers was generally observed.

We also analyzed the effect of land use in the catchment area and of the marine intrusions on the indicators of eutrophication of these coastal lagoons, using linear and nonlinear regressions. Afforestation was found to have apparently no impact on indicators of eutrophication, while agriculture had a tendency to increase the total phosphorus and suspended solids and a decrease of the total and dissolved nitrogen forms. The nutrient load per unit area exported from the

catchment area significantly increased the abundance of submerged plants and phosphorus in the sediment. Native forests have a clear effect of decreasing nutrients in the lagoons and the abundance of primary producers (excluding phytoplankton), while in contrast littoral wetlands appear to be a source of nutrients. Salinity in general was associated with low values of most eutrophication indicators. These results may be indicating that in general the nutrient load exported from the catchment areas to the coastal lagoons are moderate, but also that there are processes that decrease the values of the eutrophication indicators, such as nutrient retention in the native forest, the freshwater discharge to the ocean and the further dilution with seawater. On the contrary, the hypertrophic state of the Laguna del Diario may be explained by the substantial increase in the nutrient load exported from the catchment area due a rise in population, combined with the interruption of the lagoon's connection with the ocean. Therefore, in this lagoon the loss of the natural hydrological processes that counteract the nutrient load from the catchment area may be causing the accumulation of nutrients in the sediment and the proliferation of submerged plants.

Furthermore, we analyzed a six year series of data of abundance of submerged plants in the Laguna de Rocha to determine if plant abundance has been increasing due to the rise in nutrients. Conversely, a high fluctuation of this community and plant ephemeral proliferations were frequently observed. It was concluded that salinity is the main conditioning factor of the community and that although the effects of increased nutrients cannot be discarded they are not clearly identifiable.

We conducted an analysis of the pollen record of recent sediment of the lagoons that still connect with the ocean to determine the submerged plant composition and their relative abundance over time. We noted that submerged plants have been present in the lagoons for the last 60-80 years at least and although their relative abundance was highly variable in the pollen record no ephemeral proliferations could be detected.

The application of multi-attribute and multi-objective models in the catchment area of the largest coastal lagoons in Uruguay revealed that conflicts among current land uses occur in 4% of the area. These potential conflicts may increase to up to 20.3% of the catchment area if productive but antagonist activities such as afforestation and agriculture continue to expand into their suitable soils. This expansion is expected in the short term, given the trend of intensification of land uses in the area and the low occupancy of the suitable soils for these uses. Utilizing this methodology we obtained a map with an optimal allocation of all land uses into their most suitable lands, therefore avoiding the coexistence of competing uses for the same territory. These results are very useful in guiding the land management policies of the region, complementing the *ad hoc* methods used so far.

INTRODUCCIÓN GENERAL

Lagunas costeras

Las lagunas costeras cubren 60000 km² del planeta, ocupan 14% de su zona costera (Mitsch & Gosselink 2000) y son típicas de latitudes medias, donde la marea reducida y la acción del oleaje permite la acumulación de arena paralelamente a la costa (Nichols & Allen 1981). En particular las lagunas obstruidas son cuerpos de agua someros y salobres, separados del ambiente costero por una barrera de arena, que se conectan periódicamente con el océano por medio de un canal. En estos cuerpos de agua confluyen dos flujos de energía en constante cambio, el agua proveniente del continente y del océano. Debido a este fenómeno físico, las lagunas costeras presentan cambios muy dinámicos a nivel espacio-temporal y en sus características físicas y químicas, particularmente la salinidad. Consecuentemente, sus comunidades biológicas se encuentran permanentemente estresadas y su distribución es muy variable. Esta compleja variabilidad natural debe ser adecuadamente comprendida para utilizar y manejar racionalmente sus recursos (Laserre 1977), ya que la dinámica natural entre el medio físico y la biota es altamente vulnerable a las actividades humanas (Costanza *et al.* 1993; Kjerve 1994).

Las lagunas costeras y su zona de inundación se encuentran además entre los ecosistemas más biodiversos y productivos del planeta (Knoppers 1994) y sustentan importantes servicios ecosistémicos. La trama socioeconómica en el entorno de las lagunas costeras y sus cuencas generalmente se basa en dichos servicios ecosistémicos. Entre muchos otros bienes y servicios ambientales se destacan las pesquerías, la extracción de juncos, los valores estéticos de importancia turística, la atenuación del impacto del cambio climático, el control hidrológico, la generación y el mantenimiento de suelos y el control de especies invasoras. La mayor parte de estos servicios son económicamente invaluable, pero influyen significativamente sobre los valores económicos directos. Sin embargo, están seriamente amenazados por procesos de eutrofización antrópica, contaminación en general y urbanización en su zona adyacente, entre otros impactos humanos causados por el crecimiento poblacional en la zona costera (Estevez *et al.* 2008). Además estos sistemas suelen presentar paisajes muy contrastantes, lo que los vuelve especialmente atractivas para el desarrollo turístico y urbano.

Eutrofización de sistemas someros y estuarinos

La eutrofización en sistemas acuáticos en general, y en lagunas costeras en particular, es una de las amenazas más destacadas, que alteran el funcionamiento natural y los servicios ecosistémicos que los ecosistemas acuáticos proveen (Carpenter 2005; Conley *et al.* 2009). Uno de los impactos más relevantes de la eutrofización en estuarios y lagunas costeras es que promueve una sucesión de productores primarios, debido fundamentalmente a la competencia por luz. En aguas salobres las charofitas que forman densas matas adyacentes al sedimento son primeramente reemplazadas por especies con densa canopia superficial que les permite captar más luz (Scheffer 1998), como los géneros *Myriophyllum* o *Potamogeton*. A su vez, en un gradiente de nutrientes en el agua y en zonas más salobres, las angiospermas sumergidas y charofitas pueden ser reemplazadas por macroalgas marinas o estuarinas. El fitoplancton por su parte, puede reemplazar al resto de los productores primarios, desarrollando floraciones de algas potencialmente tóxicas (McGlathery 2001; Rabalais 2002). Estos cambios alteran el funcionamiento ecológico, modificando las tramas tróficas y por tanto comprometiendo las pesquerías costeras (McGlathery 2001; Fox *et al.* 2008). Si bien se considera al proceso de eutrofización antrópica como reversible y existen diferentes tecnologías de ingeniería (oxigenación del fondo, modificación del tiempo de residencia, secuestro de fósforo por Fe o Ca, entre otras; Eiselová (1994)) y ecotecnologías (biomanipulación, extracción de nutrientes con plantas acuáticas, entre otras) para mitigar dicho impacto en sistemas profundos y someros (Perrow *et al.* 1995), la recuperación puede tomar mucho tiempo. Carpenter (2005) reportó que en lagos eutrofizados por aportes agrícolas la recuperación puede tomar 1000 años y requiere que la concentración de fósforo en los suelos de las cuencas agrícolas sea reducida sustancialmente.

La eutrofización es la principal causa de contaminación de los sistemas acuáticos continentales y su control es un problema social mundialmente reconocido (Carpenter *et al.* 1998). Europa, Estados Unidos y Australia, entre otros, están fijando restricciones para la exportación de nutrientes hacia las aguas superficiales (e.g. USA Clean Water Act (EPA 2008), Australian and New Zealand Guidelines for Freshwater and Marine Quality (ANZECC & ARMCANZ 2000); European Water Framework Directive (Directive 2000/60/EC)). Generalmente, en estos países la principal fuente de nutrientes es difusa debido a que han establecido sistemas de tratamientos poderosos para efluentes urbanos e industriales. Por el contrario, en países de renta media las fuentes puntuales continúan siendo el principal problema debido a la falta de sistemas de tratamiento, así como al menor desarrollo agrícola. Sin embargo, en el nuevo escenario mundial de incremento de la producción agropecuaria y del traslado de la agricultura intensiva hacia el tercer mundo se espera que dicho panorama cambie considerablemente (Carpenter 2005).

Aportes de nutrientes desde la cuenca de drenaje

Como regla general, los ambientes naturales como praderas y bosques nativos exportan menor cantidad de nutrientes a los cuerpos de agua en comparación con los usos urbanos y agropecuarios (Ryding & Rast 1992; Jeje 2006). El aporte de nitrógeno desde la cuenca puede ocurrir desde cualquier punto, ya que la principal forma de llegada del nitrógeno es disuelta bajo forma de nitratos (Sharpley *et al.* 2003). Debido a la gran solubilidad del nitrato, las fuentes subterráneas o de la napa freática son las más destacadas. Por el contrario, la dinámica del fósforo está determinada por su baja solubilidad, lo que determina que la principal fuente de este nutriente sean los sólidos en suspensión, lo que requiere un proceso de transporte de alta energía, como la escorrentía superficial, para alcanzar los cuerpos de agua. Por lo tanto, el transporte de fósforo ocurre mayoritariamente desde zonas cercanas a los cuerpos de agua (Sharpley *et al.* 2003). Existen evidencias contundentes que indican que la vegetación riparia, ya sea arbórea o herbácea, disminuye el aporte de nutrientes desde la cuenca hacia los arroyos (Dodds & Oakes 2006). Una combinación de procesos físicos y biológicos promueve la retención de los sólidos en suspensión transportados por la escorrentía, mientras que las raíces incorporan las formas disueltas en el agua subsuperficial. Además, protege a las márgenes de los arroyos de la erosión fluvial y de escorrentía, así como del pisoteo del ganado (McKergow *et al.* 2003 y referencias citadas). Por otra parte, los humedales son considerados sumidero de nutrientes. El fósforo suele ser atrapado en los sedimentos oxigenados por la vegetación acuática emergente mientras que el nitrógeno disminuye a causa de la desnitrificación (Vymazal 1995; Mitsch & Gosselink 2000), por lo que se utilizan humedales artificiales para minimizar la exportación de nutrientes hacia los cuerpos de agua (Vymazal *et al.* 1998).

Los aportes de nutrientes desde los campos agrícolas están determinados por el tipo de manejo productivo. Por lo tanto, son altamente dependientes de las decisiones de los productores a escala de predio. De esta manera la mayoría de las recomendaciones y medidas para mitigar el aporte de nutrientes a los cuerpos de agua apunta a introducir el aspecto ambiental como una variable más en el manejo productivo de los predios agropecuarios. Algunas de esas medidas son llevar un sistema de cuentas del balance de nutrientes en los predios (Oenema & Roest 1998), donde se considera cuánto fertilizante se aplica, cuál es la concentración en los suelos, cuánto se remueve por cultivos y cuánto se exporta. Este es un sistema de apoyo a la toma de decisión, por ejemplo a la hora de decidir aplicar o no fertilizante. Otras medidas son la restauración del bosque ripario, construcción de humedales riparios ó la protección de las herbáceas de alto porte en el litoral de los arroyos, así como establecer exclusiones de ganado en los márgenes de arroyos para evitar su erosión, entre varios otros. Estas medidas son conocidas como Buenas Prácticas de Manejo y fueron primeramente establecidas en el "Clean Water Act" de Estados Unidos. Es muy importante destacar que todas estas medidas son impulsadas por los gobiernos e incluyen fuertes controles ante su incumplimiento, no dependiendo únicamente de la voluntad y capacitación de los propietarios o técnicos asesores.

Efectos del cambio climático

El cambio climático aparece como un forzante más de los procesos de eutrofización de los cuerpos de agua someros (Meerhoff *et al.* 2007), especialmente en países donde las predicciones son el incremento de las precipitaciones y de aumento de la probabilidad de eventos extremos como tormentas o sequías (Bouraoui *et al.* 2002). Esto implica incrementos en la escorrentía superficial que en escenarios de intensificación de los usos del suelo aumentaría la exportación de nutrientes a los cuerpos de agua. Entre el 70 y 90% del aporte de sólidos en suspensión y de fósforo a los cuerpos de agua puede ocurrir en apenas una o dos tormentas intensas al año. Por otra parte, los períodos de menor caudal de agua, si coinciden con los meses de verano, suelen tener mayores problemas de calidad del agua por el desarrollo de floraciones algales o eventos de anoxia (Jarvie *et al.* 2006). Esto se agrava considerablemente con la extracción de agua de los sistemas acuáticos para potabilización o riego.

Herramientas de planificación ambiental

El reconocimiento de los problemas ambientales y de bienestar humano asociados al manejo de los ecosistemas ha puesto en evidencia la necesidad de planificar los usos del territorio, considerando otros aspectos además de los económicos o tecnológicos. Incorporar las variables ambientales a la planificación vuelve aún más complejo el proceso. Por otra parte, la legislación internacional, incorporada gradualmente por los países en desarrollo, exige instancias de participación social como forma de legitimar los procesos de planificación. Esto aumenta un grado más la complejidad. En tal sentido, los modelos multiatributo y multiobjetivo asociados a sistemas de información geográfica están siendo crecientemente utilizados en ámbitos de planificación estratégica, evaluación de impacto ambiental, planificación de desarrollos forestales y agrícolas, diseño de áreas protegidas y logística, entre otros (Malczewski 2006). Estos modelos permiten generar y evaluar escenarios y elaborar diferentes alternativas de desarrollo territorial para consideración de los decisores (Ligmann-Zielinska *et al.* 2008), todo lo cual se convierte en un insumo fundamental para establecer planes de ordenamiento ambiental del territorio. Algunas técnicas son más convenientes para escalas regionales o de cuenca, mientras que otras son más apropiadas para escalas locales o para modelar aspectos más específicos. Estas herramientas permiten diseñar el territorio a nivel de píxeles y también de predios. Por lo tanto, generan resultados a la escala en la que se toman las decisiones cotidianas, a la vez que incorporan aspectos que operan a escalas espaciales mayores. Además, permiten instancias genuinas de consulta a los interesados, promoviendo la participación social (Bojórquez-Tapia *et al.* 2001). En tal sentido aparecen como herramientas ineludibles para planificar los usos, especialmente en países con escasos recursos que deben evaluar seriamente dónde y cómo invertir en desarrollo.

La situación de Uruguay y las lagunas costeras de la Cuenca Atlántica

Uruguay no está ajeno a la realidad internacional y regional de intensificación de los usos agrícolas y del cambio climático. Procesos de eutrofización ocurren en todo el país, en múltiples tipos de sistemas acuáticos naturales y artificiales, y parecen estar aumentando su frecuencia e intensidad (por una revisión de los casos de floraciones algales en Uruguay ver PNUMA *et al.* 2008). Pese a esto, las mejoras tecnológicas no aumentan proporcionalmente y aún se carecen de sistemas de tratamiento terciario para remover nutrientes de las aguas residuales, mientras que la incorporación de aspectos ambientales en el manejo agropecuario está siendo reciente y tímidamente considerada. Más aún, las recomendaciones de adaptación al cambio climático pueden ser contraproducentes desde el punto de vista de la calidad del agua, como las alteraciones del régimen hidrológico mediante riego y el trasvase de cuencas, la artificialización de las pasturas naturales, entre otras, mostrando que se requieren aún visiones más integradoras (PNUD 2007). En tal sentido, las cuencas de las lagunas costeras de Uruguay son un caso de estudio relevante para analizar los impactos del cambio del uso del suelo en la calidad del agua y para probar por primera vez herramientas de planificación multiatributo y multiobjetivo que consideren simultáneamente aspectos productivos, sociales y ecológicos. Estas lagunas y sus cuencas se ubican en una zona de alto valor turístico y agropecuario, y por tanto

económico, y son prioritarias desde el punto de vista de la conservación de la biodiversidad, presentando relevancia internacional para la Convención Ramsar y el Programa de Reservas de Biosfera de MAB UNESCO. A su vez, estas cuencas presentan un gradiente de usos e impactos humanos y muestran un creciente cambio de usos del suelo en el tiempo. Sin embargo, aún no han alcanzado grados de deterioro drásticos, por lo que la aplicación a tiempo de medidas de manejo adecuadas puede ser clave para que el desarrollo agropecuario y turístico del área no comprometa sus servicios ecosistémicos y valores de biodiversidad.

Aproximaciones metodológicas al estudio de ecosistemas complejos

Las lagunas costeras son ecosistemas especialmente relevantes desde el punto de vista del bienestar humano, ya que ofrecen múltiples servicios ecosistémicos ampliamente reconocidos por la sociedad, algunos de los cuales sustentan economías locales o regionales (Esteves *et al.* 2008). Si bien el funcionamiento general de las lagunas costeras es conocido y también lo es la respuesta a algunos impactos humanos como la eutrofización, su predicción es incierta, siendo prácticamente imposible estimar cuándo pueden ocurrir los cambios y qué alcances pueden tener. Las lagunas costeras son altamente complejas, ya que a la dinámica natural de los sistemas acuáticos se le impone la conexión intermitente con el océano que implica cambios hidrológicos, en la concentración de nutrientes y organismos. A esto se le suma el condicionante climático y geomorfológico como lluvias, viento, altura de las olas, baja profundidad, transporte de arena en el litoral costero (Kjerfve 1994), entre otros. Especialmente, en nuestra región el clima es muy dinámico y de difícil predicción (Baethgen 2004). Esto hace que la interpretación de los datos ecológicos de las lagunas costeras sea difícil de por sí y más complejo aún entonces, es discriminar los efectos de los impactos humanos de la variabilidad natural del ecosistema.

A la complejidad y variabilidad natural de las lagunas costeras y de los ecosistemas en general, se imponen nuevas forzantes globales. Estas son fundamentalmente el cambio en el uso del suelo, donde se intensifican y expanden usos cada vez más intensivos (Vitousek 1994), y el cambio climático que aumenta la incertidumbre y la variabilidad climática (Bates *et al.* 2008). Bajo estas nuevas forzantes se vuelve cada vez más difícil discriminar el efecto de los impactos humanos en el funcionamiento de los ecosistemas. Por estos motivos, es cada vez más relevante establecer líneas de base en los ecosistemas, pero también combinar estudios provenientes de diversas disciplinas y aproximaciones, que investiguen los procesos a diferentes escalas temporales y espaciales, analizando distintas líneas de evidencia en simultáneo.

El monitoreo a largo plazo de variables indicadoras de procesos clave en los ecosistemas permite construir series temporales de datos que pueden ser utilizadas para analizar tendencias o incluso cambios drásticos (Schmitt & Osenberg 1996) en el funcionamiento ecosistémico. Dichos cambios pueden ser a *posteriori* relacionados a otras variables ambientales también monitoreadas y obtener así posibles explicaciones. Sin embargo, las series temporales de información ecológica y ambiental son escasas especialmente en países con menor inversión en ciencia y tecnología. En tal sentido otras estrategias de investigación y líneas de evidencia deben confluir. Por ejemplo las herramientas provenientes de la paleontología son de gran utilidad, ya que las mismas pueden ayudar a entender el pasado y por tanto las causas de las tendencias observadas. También, fenómenos puntuales y poco frecuentes que son capturados durante estudios diseñados con otros objetivos pueden convertirse en evidencias importantes a la hora de interpretar las respuestas de los ecosistemas a diferentes combinaciones de factores ambientales. Estudios específicos en campo y la experimentación, desde condiciones de laboratorio altamente controladas hasta manipulaciones de campo, aportan a entender procesos puntuales. Por último, la comparación entre sistemas similares pero que han sufrido impactos diferentes o de menor importancia relativa permite agregar nuevas evidencias a la interpretación de los cambios observados. En definitiva una adecuada combinación de investigaciones realizadas a diferentes escalas espaciales y temporales contribuye sucesivamente a determinar el funcionamiento general de un ecosistema y su respuesta a los diferentes impactos humanos.

DESCRIPCIÓN DE LA TESIS

Esta tesis aborda la pregunta de cómo el cambio de uso del suelo en las cuencas de cinco lagunas costeras de Uruguay impacta en los indicadores de eutrofización de dichas lagunas. Así mismo, aplica metodologías de planificación ambiental para obtener una configuración óptima de usos del suelo que maximicen el desarrollo agropecuario y turístico a la vez que minimicen el proceso de eutrofización y pérdida de biodiversidad.

Seguido a la introducción general y la descripción de las hipótesis y predicciones suceden cuatro capítulos. En el capítulo I se analizan los cambios en los usos del suelo en los últimos 30 años en las cuencas de las lagunas costeras y se evalúa cómo ha cambiado la exportación de nutrientes hacia dichas lagunas. Posteriormente, se analizan los indicadores de eutrofización en agua y sedimento y la abundancia de las comunidades de productores primarios y se los relaciona con los usos agropecuarios, atributos naturales de las cuencas como cobertura de bosque y humedales o tipo de suelos y con la salinidad, que depende del régimen de conexión entre las lagunas y el mar. Los capítulos II y III buscan evaluar cambios en la comunidad de plantas sumergidas en el tiempo y relacionarlos con la concentración de nutrientes en el agua y el sedimento, así como con la salinidad, para determinar la posible influencia del aporte de nutrientes desde la cuenca y del régimen de conexión con el océano. Por último, el capítulo IV aplica una metodología de modelación multiatributo y multiobjetivo para establecer una configuración óptima de usos del suelo que permita minimizar los impactos del desarrollo productivo y turístico a la vez de conservar la biodiversidad y los servicios ecosistémicos que minimizan el proceso de eutrofización. Cada uno de los capítulos representa una versión avanzada de un artículo científico a ser enviado a revistas internacionales.

La tesis finaliza con una discusión general, que procura integrar y sintetizar la información generada. A modo de complemento se adjuntan tres artículos científicos (ANEXO I, II y III), publicados durante el período de elaboración de la tesis, los cuales se vinculan estrechamente con la temática de la misma.

HIPÓTESIS Y PREDICCIONES

A mediados de la década del 90 y especialmente en la primera década del nuevo milenio se observó una expansión de los usos agrícolas y una intensificación de la ganadería extensiva en Uruguay. Esto implicó un crecimiento de la agricultura, de las praderas artificiales y siembras en cobertura del 122 al 1600% (OPYPA 2009), mientras que la importación de fertilizantes se duplicó entre 2001 y 2008 (DIEA 2009). La cuenca de las lagunas costeras de Uruguay sufrió un proceso similar aunque de menor envergadura que otras zonas del país. Por otro lado, si bien la población en las cuencas se ha mantenido constante, existe una migración de población rural hacia las ciudades a la vez que nuevos balnearios se consolidan en las márgenes de las lagunas, constituyendo nuevas fuentes de nutrientes. Estas lagunas presentan indicios de un aceleramiento del proceso de eutrofización antrópica (Aubriot *et al.* 2005, Pérez *et al.* 1999, Hein datos sin publicar, Rodríguez-Gallego *et al.* 2010). La Laguna del Diario a su vez, presenta un estado hipereutrófico pero de agua clara, dominado por plantas sumergidas (Kruk *et al.* 2006). Por otra parte, la conexión bidireccional de las lagunas con el mar disminuye los valores de los indicadores de eutrofización en las lagunas debido a la descarga de agua dulce con nutrientes y sedimentos en suspensión y a la dilución generada por el ingreso de agua marina pobre en dichos nutrientes (Suzuki *et al.* 1998; Kjerfve 1994; Smakhtin 2004). Por lo tanto, la alteración de la conexión de las lagunas con el mar podría estar afectando el proceso de exportación de nutrientes al mar, especialmente en la Laguna del Diario cuya conexión natural con el Río de la Plata fue alterada sustituida por un sistema artificial de desagüe que únicamente permite la descarga de agua dulce. Así mismo, se estima que las aperturas artificiales de las lagunas que aún mantienen conexión con el Océano Atlántico están afectando el proceso de exportación de nutrientes desde las lagunas al mar, y por tanto afectando el proceso de eutrofización antrópica.

Hipótesis 1: El uso del suelo en las cuencas de las lagunas costeras de Uruguay se ha intensificado en la última década debido a la intensificación de usos agropecuarios e incremento de las poblaciones humanas promoviendo un aumento de los indicadores de eutrofización, en especial provocando la proliferación de plantas sumergidas, mientras que el intercambio de agua con el mar reduce los valores de dichos indicadores.

Predicción 1: La carga de nutrientes exportada desde las cuencas hacia las lagunas costeras aumentó entre 1974 y 2005 (capítulo I).

Predicción 2: Los usos actuales de la cuenca promueven un aumento significativo de los valores de los indicadores de eutrofización y la abundancia de las comunidades de productores primarios de las lagunas costeras, observadas mediante regresiones simples (capítulo I).

Predicción 3: La conexión de las lagunas costeras con el mar disminuye significativamente los indicadores de eutrofización, mientras que la interrupción de la misma favorece su aumento indicadas mediante regresiones simples (capítulo I).

Predicción 4: Las abundancia de plantas sumergidas se ha incrementado en la Laguna de Rocha desde 2001 hasta 2008 (capítulo II).

Predicción 5: Las hidrófitas sumergidas han colonizado recientemente las lagunas costeras y su abundancia se ha incrementado en los últimos 60 a 80 años, indicado por el incremento de la abundancia relativa del polen de las mismas en sedimentos recientes de las lagunas costeras que aún se conectan con el mar (capítulo III).

Los usos actuales en las lagunas costeras de Uruguay y sus cuencas presentan interferencias entre sí, debido a que compiten por la tierra a la vez que generan externalidades que afectan a los otros usos y a los servicios ecosistémicos. Por ejemplo, la forestación y la agricultura sustituyen ambientes naturales con importantes valores de biodiversidad a la vez que podrían comprometer la calidad del agua del sistema fluvial y las lagunas costeras, compitiendo entonces con la conservación de la biodiversidad. A su vez, podrían competir entre sí cuando los suelos tienen aptitud para ambos usos. Por otro lado, la ganadería extensiva y el turismo de baja intensidad podrían ser compatibles con los otros usos, incluso con la conservación, ya que no afectan severamente los ambientes naturales. En la zona de estudio existen conflictos de usos, por ejemplo entre conservacionistas y ganaderos que se oponen a la forestación y a la agricultura intensiva o entre los conservacionistas y el sector turístico que promueve desarrollos urbanos tradicionales. Por otra parte, se espera que los usos agropecuarios, forestales (OPYPA 2009) y turísticos (Uruguay XXI 2009) del suelo continúen intensificándose y expandiéndose, lo que además de aumentar los conflictos con el sector conservacionista promovería conflictos de uso entre los sectores de producción. Los mismos serían acompañados seguramente de problemas sociales, debido a cambios en la tenencia de la tierra, de costumbres y formas de vida, complejizando aún más la búsqueda de soluciones. La elaboración de planes de ordenamiento ambiental en consulta con los involucrados contribuiría a encontrar configuraciones espaciales de usos del suelo que permitan la co-ocurrencia de los usos actuales, incluso en escenarios de expansión de los mismos, a la vez que permitirían conservar la biodiversidad y los servicios ecosistémicos, minimizando la eutrofización de los cuerpos de agua. La legislación nacional prevé mecanismos de planificación estratégica, de generación de planes de ordenamiento territorial a diferentes escalas territoriales y de planes de manejo de áreas protegidas, todos ellos con la anuencia de los interesados. En este sentido, las metodologías de Evaluación de Aptitud de Usos del Suelo (Land Suitability Assessment) asociadas a Modelos Multiatributo, Multiobjetivo y Sistemas de Información Geográfico (Bojórquez-Tapia *et al.* 2001; 2004; Malczewski 2006) podrían ayudar a entender los conflictos actuales, elaborar escenarios de

cambios de usos del suelo y de futuros conflictos de uso, así como colaborar con la Planificación Estratégica del territorio, asegurando la participación social.

Hipótesis 2: Existen conflictos entre diferentes usos del suelo en las cuencas de las lagunas costeras con conexión al mar y se espera que se incrementen en el corto plazo, sin embargo, es posible configurar dichos usos para minimizar la eutrofización y la pérdida de biodiversidad en un contexto de expansión agropecuaria y turística.

Predicción 1: La superficie ocupada por los usos actuales en las cuencas de las lagunas costeras con conexión al océano presentan importantes interferencias entre sí, las que se incrementarían considerablemente frente a la expansión de los usos más intensivos (capítulo IV).

Predicción 2: La agrupación de los usos del suelo en las zonas con mayor aptitud para realizar dichas actividades minimiza los conflictos entre usos antagónicos (capítulo IV).

OBJETIVO GENERAL Y ESPECÍFICOS

El objetivo de este trabajo es evaluar la influencia del uso del suelo en las cuencas de cinco lagunas costeras de Uruguay en los indicadores de eutrofización, determinar el efecto de la conexión con el mar en dichos indicadores y la configuración óptima de usos que minimice el proceso de eutrofización y la pérdida de biodiversidad.

Objetivos específicos

1.1. Determinar los cambios en el uso del suelo en los últimos 30 años en las cuencas de cinco lagunas costeras de Uruguay, mediante análisis de imágenes satelitales y de censos agropecuarios y de población.

1.2. Estimar la carga total de nutrientes exportada desde las cuencas a las lagunas y determinar su evolución temporal, mediante la aplicación de coeficientes de exportación específicos a los diferentes usos.

2.1. Estimar indicadores de eutrofización en diferentes zonas de las lagunas costeras durante un año y medio, tanto en el agua (nutrientes totales y disueltos), el sedimento (nutrientes y materia orgánica) como en las comunidades de productores primarios más abundantes (hidrófitas sumergidas, fitobentos y fitoplancton), así como de otras variables limnológicas relevantes como salinidad, oxígeno disuelto y sólidos en suspensión, entre otras.

2.2. Determinar el efecto de los usos del suelo y de las características de las cuencas en los indicadores de eutrofización en las lagunas costeras.

3. Determinar el efecto de la conexión con el mar (utilizando la salinidad como indicador del grado de conexión) en los indicadores de eutrofización en las lagunas costeras.

4. Determinar variaciones en la abundancia de plantas sumergidas en la Laguna de Rocha, utilizando una serie temporal de seis años y relacionarlas con los indicadores de eutrofización y con la salinidad del sistema.

5. Determinar si las plantas sumergidas son colonizadoras recientes, si muestran una tendencia de aumento en los últimos años y si han presentado proliferaciones esporádicas recurrentes a partir del análisis del registro polínico de los sedimentos depositados en las últimas décadas en las lagunas con conexión con el océano.

6.1. Determinar la aptitud del suelo y su distribución espacial para los usos más relevantes en las cuencas de las lagunas costeras que aún se conectan al océano, mediante un modelo multi-atributo.

6.2. Analizar los conflictos de usos del suelo actuales y potenciales de mantenerse la tendencia actual de intensificación de la producción agropecuaria, forestal y turística, empleando modelación multi-atributo.

7. Zonificar las cuencas en función de su aptitud para todos los usos del suelo utilizando modelación multi-objetivo y optimizar la aptitud total del territorio restringiendo los usos antagónicos mediante programación lineal.

CAPÍTULO I: Effects of land use changes on eutrophication indicators in five coastal lagoons of the SW Atlantic

Lorena Rodríguez-Gallego

ABSTRACT

Awareness about the over-enrichment of surface waters from agricultural nutrients is increasing and gaining attention worldwide. Generally, natural grasslands and forests export fewer nutrients than agricultural lands, animal intensive production systems and urban zones. Therefore, changes in management practices at the farm scale and sewage treatment are required to minimize nutrient export. However, in order to select and prioritize management recommendations it is necessary to know the main sources and pathways of the exported nutrients. One way to calculate a general approximation of the exported nutrients is to estimate their annual load in selected water bodies and to assign export coefficients to different aerial extensions of particular land uses, on a catchment or sub-catchment scale. Uruguay's coastal lagoons were selected to conduct a nutrient exportation analysis to surface waters. These five lagoons are important sites for biodiversity conservation and are protected by national legislation and international conventions (Ramsar and MAB Unesco Biosphere Reserve Program). However, land use intensification driven mainly by agriculture and tourism development is increasing the risk of eutrophication. Using satellite images and national agriculture censuses, a quantitative analysis of land use changes from 1974 to 2005 was conducted and a nutrient export coefficient approximation was used to determine the changes in annual loads over time. At the same time, an assessment of several eutrophication indicators (water, sediment and autotrophic communities) was carried out seasonally in the lagoons' basins during 2005 and 2006. Eutrophication indicators were related to catchment area characteristics and land uses through linear and non-linear regressions. The aerial annual load of nutrients exported to the lagoons increased over time, with population and extensive livestock ranching being the most important nutrient sources. Agriculture could also become an important source if intensification continues. The important buffer effects of riparian forests on eutrophication indicators were observed, while wetlands surrounding the lagoons played secondary and complex roles. Afforestation was not found to impact eutrophication indicators, while phosphorus concentration increased with agriculture. Salinity was a major determinant of eutrophication indicators, suggesting that the manipulation of the natural connection between the ocean and the lagoons is a critical management issue. These results are useful for generating general recommendations to prevent eutrophication, but are most important for establishing a guideline to promote new areas of research and establish priorities. Research on the mechanisms involved in the buffer capacity of the riparian forest, the nutrient source or sink role of wetlands and the denitrification process are needed.

Key words: nutrient load, eutrophication indicators, coastal lagoons, Uruguay.

INTRODUCTION

Reduction of anthropogenic eutrophication is increasingly being considered by nations worldwide (e.g. USA Clean Water Act (EPA 2008), Australian and New Zealand Guidelines for Freshwater and Marine Quality (ANZECC & ARMCANZ 2000); European Water Framework Directive (Directive 2000/60/EC), etc.). Among the first actions taken to decrease this process was the control of point sources through the establishment of sewage and industrial effluent treatment plants. Unfortunately, water quality and the ecological health of rivers and lakes have not recovered to acceptable levels in all cases. Therefore, efforts are now being taken to control diffuse sources of nitrogen and phosphorus mainly from agricultural lands (Sharpley *et al.* 1999) and best management practices are being promoted (*sensu* the USA Clean Water Act) at the farm scale (Oenema & Roest 1998; Sharpley *et al.* 2003).

It can take lakes up to 1000 years to recover from eutrophication caused by agricultural nutrient over-enrichment of soils (Carpenter 2005). In these systems, the slow decrease of phosphorus in the soil in the catchment area retards recovery from eutrophication, although nutrient recycling from sediments can further delay the process (Carpenter 2005). Generally, agricultural lands export higher levels of nutrients than natural forests and grasslands (Ryding & Rast 1992; Jeje 2006). Therefore, aquatic ecosystems located in agricultural catchment areas tend to be more

eutrophic than those in natural landscapes. However, mechanisms exist at the scale of catchment areas to buffer upland runoff entering surface waters. Riparian vegetation can improve stream water quality through a combination of physical, chemical and biological process. This vegetation stabilizes river banks, protecting them from fluvial and runoff erosion, and also filter and trap upland sources of sediments, nutrients and other chemicals (McKergow *et al.* 2003). Also, wetlands can act as important sinks for nutrients and suspended solids, although their specific role can vary from system to system (Mitsch & Gosselink 2000).

Natural grasslands constitute the dominant ecosystem in Uruguay (savannas *sensu* Olson *et al.* 2001), covering more than 70% of the country's surface area (ca. 11.6 million ha) according to DIEA (2000). Temperate grasslands are one of the most threatened biomes in the world (Hoekstra *et al.* 2005). Natural grasslands in Uruguay are home to a rich variety of herbaceous plants (more than 400 species of grasses, MVOTMA *et al.* 1999), making them a high priority for biome conservation. Natural forests are mainly restricted to the riparian zones of the extensive fluvial system and to the rocky hills, covering a surface area of ca. 4% of the national territory (Nebel 2004). The most important economic activity in Uruguay is livestock ranching, which is still conducted extensively on natural prairies. Meat represents the most important export product (20% of total goods export, Uruguay XXI 2009). Over the last decade, livestock ranching intensified while agriculture expanded. Surface area of artificial prairies increased 122%, soybean 1100% and wheat 1600%. Afforestation (the conversion of grasslands and shrublands to tree plantations, *sensu* Farley *et al.* 2005) with exotic trees for wood and pulp mill production increased 271% from 2002 to 2009 (OPYPA 2009). Fertilizer imports doubled between 2001 and 2008 (DIEA 2009). Sanitation service is concentrated in urban zones and achieves 56.5% of the total population, while 41.9% use septic tanks. However, the tertiary treatment systems necessary to remove nutrients from the sewage are lacking and sewage is generally diverted into rivers. Although industry is not strongly developed in Uruguay, it can be considered an important point source of nutrients in several streams and rivers in the country.

Land use intensification has been accompanied by water quality deterioration, and algal blooms have become a frequent phenomenon in Uruguayan freshwater and brackish ecosystems, including those used to supply drinking water for humans and cattle (PNUMA *et al.* 2008). Despite the fact that cultural eutrophication symptoms are already evident in aquatic ecosystems, present levels of deterioration are still lower than those in developed countries. The early application of best management practices for the agricultural sector and improvements in sewage treatments, accompanied by strict controls, should be effective in preventing further water deterioration. The risk of water quality deterioration may be enhanced by climatic change. Predictions for Uruguay suggest an increase in rainfall and runoff, with high probabilities of extreme rainfall as well as droughts (PNUD 2007). Climatic change could intensify the hydrological cycle, thus increasing the recycling and transport of nutrients from agricultural areas affecting water quality (Bouraoui *et al.* 2002). Nutrient budget assessments at the catchment scale could provide insights into the best recommendations for minimizing eutrophication and confronting climatic changes.

The aim of this study was to: 1) assess land use changes in the basin of five coastal lagoons in Uruguay (Laguna del Diario, Laguna José Ignacio, Laguna Garzón, Laguna de Rocha and Laguna de Castillos), 2) estimate the annual nutrient loads to surface waters; and 3) analyze the effects of current land use on eutrophication indicators. An export coefficient approach was used to estimate the export of nutrients to lagoons, based on the surface area of each land use and specific export coefficients for nitrogen and phosphorus. This approach does not require detailed in-stream chemical or water discharge data and it can be used to assess the effects of changes in land use on nutrients loads (May *et al.* 2001).

METHODOLOGY

Study area

On the Atlantic coast of Uruguay there is a series of coastal lagoons that periodically connect to the ocean through a breach which opens on their sand bars (Fig. 1, Table 1). In the case of Laguna de Castillos, the connection with the ocean occurs by way of the Valizas stream that also periodically opens to the ocean through a breach on the sand bar. Such natural dynamics drive steep salinity gradients and determine the ecological functioning of the entire ecosystem (Conde *et al.* 2000; 2002), affecting the abundance and composition of phytoplankton (Bonilla *et al.* 2005), phytobenthos (Conde *et al.* 1999), bacteria (Piccini *et al.* 2006), benthos (Pintos *et al.* 1991) and submerged aquatic vegetation (Rodríguez-Gallego *et al.* 2010). The connection with the ocean is often artificially forced by the local municipalities in order to reduce flooding in mostly unplanned urbanizations. The natural connection of Laguna del Diario with the ocean was replaced by a permanent outlet of freshwater discharge into the ocean, when a coastal route was built in the 1950s. As a result, marine intrusions and the occurrence of a salinity gradient have been impeded in this lagoon.

The coastal lagoons catchment area is dominated by grasslands mixed with patches of mainly riparian and sierra forests. Large areas of freshwater and saline wetlands surround the lagoons and sand dunes are abundant in the coastal zone. These dunes were partially fixed by exotic trees and shrubs planted (*Pinus* spp. and *Acacia* spp.) at the first half of the 20th century. These lagoons sustain ca. 57% of Uruguay's bird species (Aldabe *et al.* 2006) and several endemic species of vertebrates, invertebrates and plants, as well as relict and endangered forests (e.g. palm tree forests and coastal forests and shrublands). Important ecosystem services are provided by these systems and their catchment areas. The lagoons are reproductive, nursery and feeding areas for coastal fish (e.g. white croaker, kingfish, flatfish) (Fabiano *et al.* 1998; Vizziano *et al.* 2002; Norbis & Galli 2004) and crustaceans (blue crab and pink shrimp), which sustain several coastal inland artisanal fisheries (Fabiano & Santana 2006). The outstanding landscape values of these lagoons are a major target for the growing tourism industry. The coastal lagoons are also part of the Biosphere Reserve (MAB-Bañados del Este) and include the first Ramsar site in Uruguay, and are presently being inducted into the National System of Natural Protected Areas (SNAP). Recent studies positioned these lagoons within the highest priority areas for biodiversity conservation (Brazeiro 2008).

The population in the study area is relatively low (38,357 inhabitants; 91.6% urban) and the density is ca. 1 person per 10 ha (Table 1). The most important land uses are livestock ranching (72.7 % of the surface area, DIEA 2000) on natural prairies, agriculture, afforestation, tourism, artisanal fisheries and biodiversity conservation. However, in the 1990s intense land use changes began to occur. Agriculture is expanding and afforestation with exotic species (eucalyptus and pine) was established as a new economic activity. In the coastal zone, urbanization for tourism is increasing the population density and small villages (whose populations increase 10 times during summer) are encroaching into natural areas, with some sites becoming permanently inhabited. This process of land use intensification is also increasing the infrastructure and the demand for services.

Major environmental concerns in these lagoons include nutrient increases due to runoff from agricultural lands and urban zones, over-fishing (Fabiano & Santana 2006) and hydrological alterations, all driving biodiversity loss as well as landscape homogenization. Eutrophication is among the most critical threats to Uruguay's coastal lagoons. Laguna del Diario is the clearest example of the result of an unplanned development in the catchment area of a lagoon ecosystem. This lagoon developed an accelerated eutrophication process, with submerged aquatic vegetation (SAV) completely covering the lagoon and anoxic sediments that are rich in organic matter (Kruk *et al.* 2009). The alteration of the natural connection with the ocean, increased urbanization in the catchment area and the use of fertilizer in nearby residential areas, are among the main causes of this cultural eutrophication process.

Eutrophication indicators suggest that Uruguay's other coastal lagoons are also in the initial phases of cultural eutrophication. Phosphorus appears to be increasing in the Laguna de Rocha (Aubriot *et al.* 2005), possibly due to runoff from agricultural lands (Rodríguez-Gallego *et al.* 2009), although the role of inputs from the Rocha city (25,000 inhabitants) should not be ignored. Additionally, blooms of potentially toxic cyanobacteria have already been observed in Laguna de Castillos (Pérez *et al.* 1999, Bonilla com. Pers. 2010) and in Laguna de Rocha (V. Hein, unpublished).

Land use classification and estimation of nutrient budget

We quantified land use changes over a 31 year period by comparing Landsat satellite images from 1974 (Path/Row 222-084, resolution of 70 m²), 1997 (Path/Row 222-084, resolution of 25 m²) and 2005 (Path/Row 222-084, resolution of 25 m²). We selected these images because we wished to: 1) obtain the oldest Landsat image available for the study area and therefore capture the largest possible period of time, 2) analyze the land use changes during 1996 that could have promoted the SAV proliferation recorded in the Laguna de Rocha during that summer; and 3) analyze the land uses changes at the beginning of this study.

Table 1. Physical and socioeconomic description of the coastal lagoons of Uruguay and their catchment areas.

	Diario	José Ignacio	Garzón	Rocha	Castillos
Lagoon area (ha)	53	1565	1503	7304	7900
Catchment area (ha)	2485	70358	56055	121433	136665
Human settlements and other relevant tourist area	Influence of the towns Los Aromos, Villa Delia, Los Corchos and Punta del Este	J. Ignacio village, Santa Mónica and Eden Rock seaside resorts, influence of La Barra and J. Ignacio tourist area	Garzón village, influence of La Barra and J. Ignacio tourist area	City of Rocha, influence of the town of La Paloma	City of Castillos, 19 de Abril village, influence of the villages of Valizas, Cabo Polonio and Aguas Dulces
Inhabitants (2004 census)	1454	893	546	26735	8874
Mean depth and range between brackets (m)	1.6 (1.1 to 2.0)	0.5 (0.2 to 1.5)	0.9 (0.1 to 2.7)	0.5 (0.1 to 1.3)	1.0 (0.3 to 1.7)
Distance from the central point of the lagoon to the sea (km)	0.95	3.851	5.12	7.57	13.87
Total length of the fluvial system (km)	41.6	1513.8	1098.2	2310.6	2728.0
Drainage density	1.67	2.15	1.96	1.90	2.00
Wetlands/Lagoon surface	3.0	0.6	1.1	0.4	1.7
Catchment/Lagoon surface	46.88	44.95	37.29	16.63	17.30
Perimeter of the lagoon (km)	4.7	47.5	56.3	86.3	58.6
Maximum length of the lagoon (km)	1.7	5.7	7	15.5	12.9
Flooded soils (ha)	217.8	2651.2	3239.1	9076.4	13890.9
Highland soils (ha)	177.3	38105.8	16126.8	41054.9	36353.3
Soils suitable for agriculture (ha)	1916.4	26333.2	32707.2	61646.8	58938.7

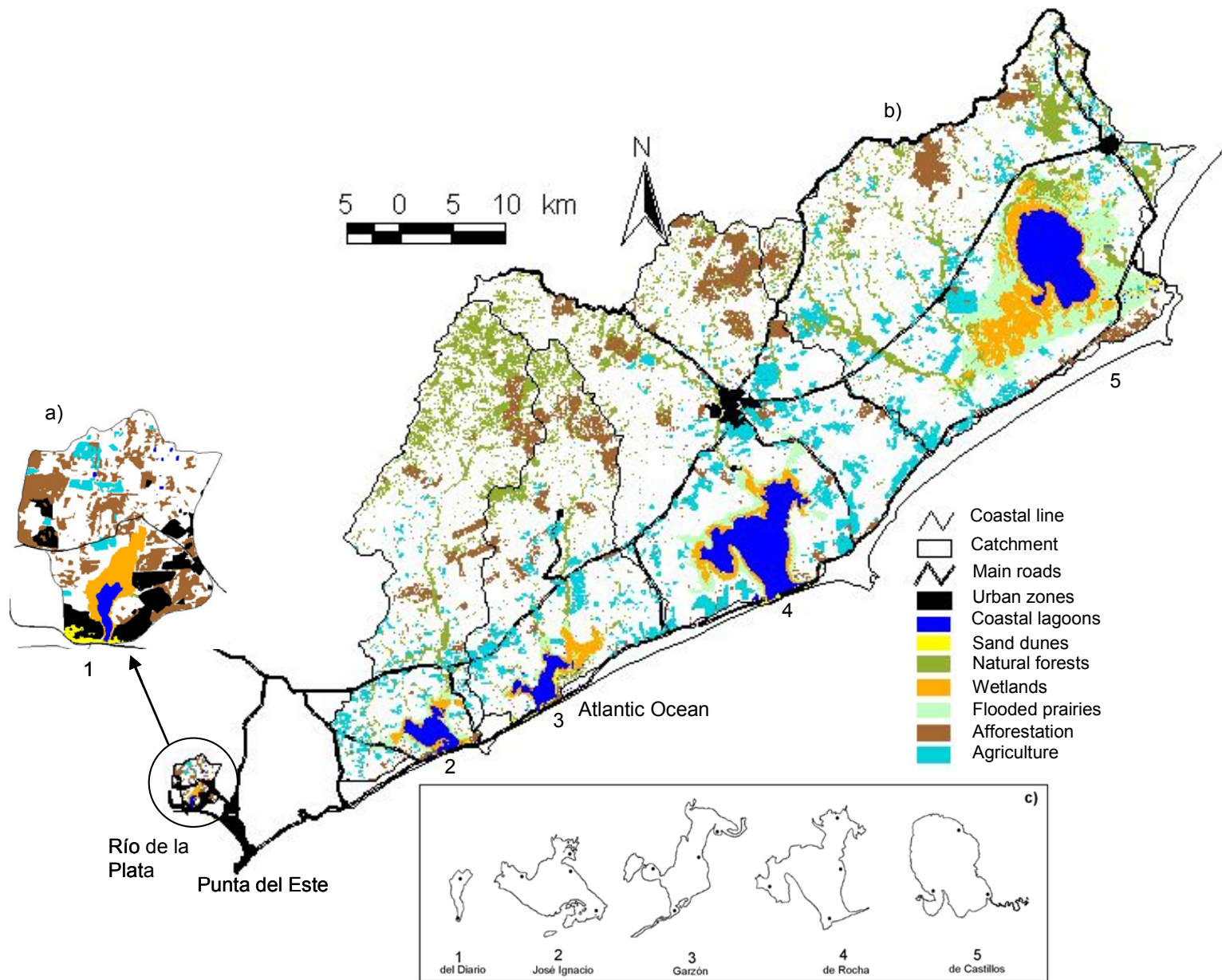


Fig. 1. Map of the study area. The basin of the coastal lagoons, main routes and towns, the location of the dominant ecosystems, afforestation and agriculture are indicated. In the inset, the sampling points of the water quality survey in each lagoon are also shown. On the main map, the white color represents grassland areas.

All images corresponded to the summer. We determined the land uses and main ecosystems using a combination of automatic and supervised techniques. The land use categories were: afforestation, lagoon surfaces (including Valizas stream), mobile or semi-vegetated sand dunes, natural forests, wetlands, flooded prairies, urban areas, agriculture and grasslands. Agriculture grouped strictly agricultural activities, as well as artificial prairies, tilled lands, fallows and also recently fertilized grasslands and oversowing areas. The grassland surface was calculated as the remainder of the area that did not belong to any of the other categories, and was mainly dominated by natural grasslands under extensive livestock ranching, but may also include abandoned agriculture fields *sensu* the above definition. The classification was checked in the field and 1200 evenly distributed points were inspected. Classification errors were estimated in 12% of the check points. Google Earth Pro images and aerial photographs were also studied. To conduct all spatial and GIS analyses we represented the spatial attributes in vector format and used ArcView 3.2 software and the extensions Spatial Analysis and Image Analysis (ESRI), the Viewshed function of the extension Spatial Analyst of ArcGIS 9.2 (ESRI) and Polygeom (Infremer). Other cartographic information was obtained from the Geography Department of the Faculty of Sciences, the Military Geographic Service, the Ministry of Transport and Public Works, the Ministry of Agriculture, Livestock and Fisheries and the National System of Protected Areas (SNAP).

To obtain a more detailed picture of agricultural uses the National Farming Censuses of 1970, 1990 and 2000 (DIEA 1970; 1990 and 2000) were consulted. Since the spatial unit changed between censuses we calculated the proportion of the spatial unit of each census occupied by the different land uses and then extrapolated to our agriculture map. The land uses considered were horticulture crops, cereal crops, forage crops, fallow, artificial prairies, oversowing and natural grasslands. The population number was obtained from the National Census of Population and Housing from 1985, 1994 and 2004 (INE 1985; 1994; 2004). Digital data of previous population censuses were not available. For both the farming and the population census the spatial units did not match with the drainage catchments of the lagoons, therefore land uses and population were assigned proportionally to each catchment area.

Once we obtained the surface area of the main land uses we applied nitrogen and phosphorus exportation coefficients to calculate the annual export of nutrients from the catchment area to each coastal lagoon and in each period analyzed. The nutrient exportation coefficients used were taken from international scientific sources and were selected by the Soil Department of the Faculty of Agronomy – Universidad de la República (Table 2). Soil groups were obtained from CONEAT (1976), and were clustered into three categories according to their characteristics and agriculture suitability: flooded soils, highlands soils and agriculturally suitable soils.

Table 2. Nutrients export coefficients, most probable values for Uruguay.

Land uses/classes	N (kg ha ⁻¹ y ⁻¹)	P (kg ha ⁻¹ y ⁻¹)	Reference
Horticulture	26.00	2.70	Word (1986 in Marston <i>et al.</i> (1995)
Cereals (sorghum, soybean)	15.40	4.11	Marston <i>et al.</i> (1995)
Forrage (oats, wheat)	7.35	0.35	Marston <i>et al.</i> (1995)
Tilled lands	7.35	0.85	Marston <i>et al.</i> (1995)
Stover	3.20	1.10	Jones <i>et al.</i> (1985) in Marston <i>et al.</i> (1995)
Artificial prairies, over sowing, fertilized prairies	6.92	1.16	Reckhow <i>et al.</i> (1980)
Grasslands	1.33	0.24	Adaptado de Drewry <i>et al.</i> (2006)
Natural forests	0.44	0.01	U.S.EPA (2002)
Afforestation	1.85	0.29	Barreto (2008)
Wetlands	0.55	0.01	Jeje (2006)
People, with septic tanks	10.4	1.6	Ryding & Rast (1992)

Water quality, sampling design and estimation techniques

We conducted a seasonal sampling between the summer of 2005 and autumn 2006 (six sampling events) in the five coastal lagoons. The spatial location of samples was designed to capture the salinity gradient, the input of the main tributaries and the presence of SAV (i.e. sites where submerged plants were usually collected with the Ekman grab). Generally, we collected samples in seaward, middle and inward zones; in inward zones samples were taken near the outlet of the main tributaries and in all cases in zones where SAV is frequently found (except in Laguna José Ignacio where SAV was absent during the study period). In Laguna José Ignacio, Garzón and Rocha we selected four sampling sites: two inward bays, the middle and seaward zones. In Laguna del Diario we only took samples in the seaward and inward zones, because a middle zone is not definable due to the lack of a salinity gradient. In Laguna de Castillos a seaward zone was not sampled because according to the morphology of the system this zone would theoretically be located in the Valizas stream, which has fluvial dynamics (Fig. 1). Three replicates were collected in each sampling site for all variables.

We collected SAV samples for biomass estimation (above and below ground) with an Ekman grab equipped with a net attached to its upper mouth. When plants reached the water surface, the grab was carefully handled to avoid material loss. Three random replicates were taken in each site. SAV biomass was washed to remove sediments and dry weight was estimated after drying for 48 hours at 80 °C. Phytoplankton samples were also collected in the same sampling points as water samples to determine biovolume and taxa composition, data are fully analyzed in Vidal (2008). *In situ* variables were also measured by triplicate with field equipment in the same sampling points. The variables were depth, pH, temperature, dissolved oxygen, conductivity (K, as an indicator of salinity), and photosynthetically available radiation (PAR, to derive PAR attenuation coefficients $K_{d\text{ PAR}}$).

Water samples were collected at ca. 10 cm depth with a Ruttner bottle, after verifying complete mixing of the water column by checking temperature and conductivity every 20 cm. We also analyzed total suspended solids (SS; APHA 1985), ammonium (NH_4 ; Koroleff 1970), nitrite (NO_2 ; Strickland & Parsons 1972), nitrate (NO_3 ; Mackereth *et al.* 1978), total nitrogen (TN; Mackereth *et al.* 1978), soluble reactive phosphorus (SRP; Murphy & Riley 1962), total phosphorus (TP; Valderrama 1981) and chlorophyll *a* (Chl *a*; acetone 90% Lorenzen method 1967). Dissolved inorganic nitrogen (DIN) was estimated as the sum of NH_4 , NO_2 and NO_3 forms. Sediment samples were manually collected down to a depth of 2 cm using acrylic corers (5 cm in diameter). The organic content of the sediment was determined by ignition (OMsed; APHA 1985), TN (TNsed) and TP (TPsed) according to Valderrama (1981) and microphytobenthos abundance was estimated using chlorophyll *a* extraction with acetone 90% (Lorenzen 1967). Sediment samples were collected for granulometry with the Ekman grab and 100 g of dry sediments were screened in a sieving rot-up system. The Udden/Wentworth (Bale & Kenny 2005) scale was used to estimate the different granulometry classes that were expressed in %. Precipitation and air temperature data were obtained from the National Meteorological Service Station in Rocha. The state of the sand bar (open or closed) was visually inspected during each sampling event. TN, TP, NID, SRP, Chl *a* of phytoplankton and phytobenthos and SAV biomass were used as eutrophication indicators.

Data analyses of water quality and land uses

To analyze the relationships among water-quality variables we conducted simple Spearman correlations and explored their spatial and temporal variability using box plot diagrams. To determine the relationships between the catchment area attributes (catchment area, land uses and natural ecosystems extension, soils types and population) with eutrophication indicator variables we conducted linear and non linear regression analysis. To do so we first averaged all water quality data of each lagoon to obtain a unique and representative value per lagoon.

RESULTS

Land use in the catchment area of the coastal lagoons

The most extended ecosystem in the catchment area of Uruguay's coastal lagoons was the grassland ecosystem (Figs. 1, 2a and b, Table 3), ranging from 64.5 to 76.1% of the total area where extensive livestock ranching represented the main land use. Cow and sheep density ranged from 0.5 to 0.7 and from 0.7 to 1.0 animals per ha, respectively. Natural forests were the second most abundant natural ecosystem, mainly composed of riparian and sierra forests, followed by wetlands (Figs. 1, 2a, 2b, Table 3). The Laguna de Castillos area presented the largest wetlands and Laguna José Ignacio the largest natural forests. Laguna del Diario presented lower grassland surface (Table 1), lower cattle density (0.1 cow per ha) and an almost complete lack of natural forests since 1974.

The main land use change between 1974 and 2005 was afforestation. Almost absent in the 1970s, this land use extended to 4 to 7 % of the lagoons' catchment area in 2005, except in Laguna del Diario which was afforested in the 1940s (Table 3). Agriculture also increased, reaching 4.9 to 9 % of the catchment area in 2005, except in Laguna del Diario where the historical 4% of agriculture was maintained. The rate of increase in agriculture was higher for Laguna de Rocha and Garzón. Furthermore, in some cases land being used for agriculture is increasingly closer to the shores of the lagoons (e.g. Laguna de Rocha). Land use in different zones is determined according to soil suitability, with agriculture conducted in middle and low lands, afforestation in the highlands and also in coastal sandy soils, and livestock ranching in the entire terrestrial zone and also in wetland areas. Changes in land use accelerated mainly after 1996, especially in the case of afforestation.

Generally, the surface area of natural ecosystems (natural forests, grasslands, wetlands, lagoons, sand dunes and flooded prairies) in the catchment area of the lagoons was maintained over time. The exception was Laguna de Castillos where some patches of natural forests were replaced by afforestation and sand dunes were increasingly covered by exotic vegetation, but in relatively small extensions. Grasslands however decreased as agriculture and afforestation increased. Urbanization and population increased only marginally in the catchment area of the largest lagoons due to urban expansion and the creation of new touristic villages. However, in Laguna del Diario urban expansion was the major land use change increasing from 0.6 to 13.9% of the catchment area (Table 3), while population increased from 250 to 1154 inhabitants (Fig. 2a, 2b). This major change was accelerated mainly after the 1990s and in summer time the inhabitant number is much higher.

When comparing the annual nutrient load potentially exported by the different land uses and population, natural grasslands and population were by far the most important nutrient sources, even higher than the agriculture uses (Fig. 2c-2f). In second place, were the fertilized grasslands and oversowing, artificial prairies and afforestation. Nutrient loads increased towards 2005, with a decrease in 1990 mainly in Laguna de Castillos (Fig. 3). Laguna del Diario showed a completely different picture: the main nutrient loads belonged to grasslands in 1974 but progressively human population became the main source, representing 75% of the current total nutrient load. The catchment area of Laguna del Diario showed the highest level of nutrient exportation per surface unit, followed by Laguna de Rocha. In all cases annual nutrient loads per ha increased over the last decade.

Environmental variables and eutrophication indicators in the coastal lagoons

Mean daily air temperature during 2005 and 2006 ranged from 11.4 to 23.1 °C (data taken from Rocha meteorological station), while annual average precipitation was 1400 mm and did not show any seasonal pattern. During 2005 and 2006 sampling period the connection with the ocean had different regimes: Laguna José Ignacio and Garzón were closed most of the period except in April 2005, while Laguna de Rocha and Castillos were opened half of the samplings occasions. Laguna del Diario was deepest (mean depth 1.6 m) and had a low water level fluctuation (Table 1). The other lagoons showed steep depth fluctuation over time. Polymixis and dissolved oxygen saturation were always registered, while pH was close to neutrality in all lagoons, except Laguna del Diario where basic conditions prevailed (8.1 ± 0.8).

Conductivity (K) exhibited a clear spatial pattern in the lagoons that periodically connect with the ocean (Fig. 3). Generally, K decreased from seaward (South) to inward (North) zones. Except in Laguna de Castillos, the northwestern stations usually had higher K values than the northeastern zones, where the higher order streams were located. All these lagoons were brackish, but freshwater and less frequently marine conditions were also observed. Laguna de Castillos and Garzón had lower K than Laguna de Rocha and José Ignacio. On the other hand, Laguna del Diario was a freshwater lagoon, with K slightly increasing towards the inward zone.

Eutrophication indicators followed an inverse pattern that K, with higher values in inward zones, but high variability was recorded (Fig. 4). TP decreased from inward to central zones and then increased again to the seaward station, except in Laguna de Rocha. The highest values were observed generally in the western and seaward stations; Laguna de Rocha and Castillos showing the highest values. TN showed similar concentrations in most stations and lagoons, except in Laguna de Castillos and del Diario where concentrations were higher. Mean concentration and standard deviation of TP and TN for all lagoons were 37.8 ± 27.2 and $422.1 \pm 342.9 \mu\text{g l}^{-1}$, respectively. SRP showed a similar spatial pattern than TP and mean concentration for all lagoons was $14.0 \pm 12.7 \mu\text{g l}^{-1}$. NID values were very low in most sampling stations ($26.2 \pm 36.1 \mu\text{g l}^{-1}$) except for some outliers in Laguna del Diario and de Castillos (data not shown). Total nutrients in the sediment were highest in Laguna del Diario, increasing slightly from seaward to inward zones, with mean values for TP_{sed} and TN_{sed} of 535.2 ± 153.7 and $1751.8 \pm 224.8 \mu\text{g gDW}^{-1}$, respectively. In the other lagoons, nutrients in the sediments were lower than in Laguna del Diario (mean values for TP_{sed} and TN_{sed}: 164.5 ± 102.9 and $297.3 \pm 341.5 \mu\text{g gDW}^{-1}$, respectively), generally increasing from seaward to inward zones. Regressions among K and eutrophication indicators were significant for DIN, TN and TP_{sed}. The relationships of K with the explanatory variables were negative, except for phytoplankton Chl *a*, that increased with K (Fig. 5A). A tendency of SS to increase with K was observed (data not shown).

Photosynthetic communities were highly variable among lagoons. SAV abundance reached maximum values in Laguna del Diario and macrophytes were present during the entire year (Fig. 4d). Intermediate biomass values were found in Laguna Garzón in only one sampling station, SAV was registered in summer and autumn in Laguna de Castillos, while it was completely absent in Laguna José Ignacio. In Laguna de Rocha SAV biomass was found in all stations over the year, with decreasing values seaward. Phytoplankton chlorophyll *a* was also highly variable among zones and lagoons, with higher levels in Laguna de Rocha (Fig. 4e). Generally, chl *a* increased from seaward to inward zones, where western stations showed maximum values. The mean phytoplankton Chl *a* concentration for all lagoons was $4.85 \pm 4.8 \mu\text{g l}^{-1}$. Cyanobacteria were found in low abundance and represented less than 3% of total phytoplankton biovolume (data not shown). The relative biovolume of this group was higher in the western stations of Laguna de Castillos, Laguna de Rocha and Laguna del Diario. The main taxa found for this group were *Aphanocapsa* sp., *Aphanothece* sp., *Pseudanabaena* sp., cf. *Limnothrix* sp. and cf. *Planktolyngbya* sp.,. Finally, microphytobenthos biomass was higher in Laguna del Diario and Laguna Garzón, and generally decreased from inward to seaward zones (Fig. 4f) with an average Chl *a* concentration of $29.3 \pm 34. \mu\text{g gDW}^{-1}$ for all lagoons.

Table 3. Land use changes from 1974 to 2005 in the catchment area of Uruguay's coastal lagoons. Land use areas are indicated in ha and the percentage of the catchment area used is shown in brackets.

		Agriculture	Afforestation	Natural Forests	Wetlands	Sand Dunes	Grasslands	Urban zones
L. del Diario	1974	103 (4.1)	318 (12.8)	2 (0.1)	122 (4.9)	86 (3.4)	1758 (70.8)	16 (0.6)
	1997	125 (5.0)	833 (33.5)	1 (0.1)	129 (5.2)	26 (1.0)	956 (38.5)	342 (13.8)
	2005	105 (4.2)	639 (25.7)	1 (0.1)	161 (6.5)	26 (1.0)	1154 (46.4)	345 (13.9)
L. José Ignacio	1974	1141 (1.6)	588 (0.8)	17335 (24.6)	658 (0.9)	166 (0.2)	48397 (68.7)	0.0
	1997	1640 (2.3)	1106 (1.6)	12044 (17.1)	876 (1.2)	159 (0.2)	52814 (75.1)	0.0
	2005	3488 (5.0)	4360 (6.2)	14553 (20.7)	919 (1.3)	126 (0.2)	45347 (64.5)	0.0
L. Garzón	1974	1975 (3.5)	278 (0.5)	6807 (12.1)	1840 (3.3)	315 (0.6)	43122 (76.9)	18 (0.0)
	1997	1837 (3.3)	1183 (2.1)	7124 (12.7)	1782 (3.2)	254 (3.2)	42163 (75.2)	18 (0.0)
	2005	4561 (8.1)	4221 (3.3)	5737 (10.2)	1627 (2.9)	269 (2.9)	38119 (68.0)	18 (0.0)
L. de Rocha	1974	6486 (5.3)	15 (0.0)	6219 (5.1)	2326 (1.9)	362 (0.3)	96191 (79.2)	835 (0.7)
	1997	7462 (6.2)	273 (0.2)	5387 (4.4)	2461 (2.0)	326 (0.3)	96846 (79.8)	1176 (1.0)
	2005	10922 (9.0)	8578 (7.1)	6308 (5.2)	2906 (2.4)	272 (0.2)	83912 (69.0)	1176 (1.0)
L. de Castillos	1974	3425 (2.5)	632 (0.5)	12926 (9.5)	14706 (10.8)	2624 (1.9)	94135 (68.9)	244 (0.2)
	1997	6243 (4.6)	1900 (1.4)	10641 (7.8)	13324 (9.6)	1733 (1.3)	94524 (69.1)	410 (0.3)
	2005	9432 (6.9)	5983 (4.4)	9539 (7.0)	13359 (9.8)	1319 (1.0)	88726 (64.9)	408 (0.3)

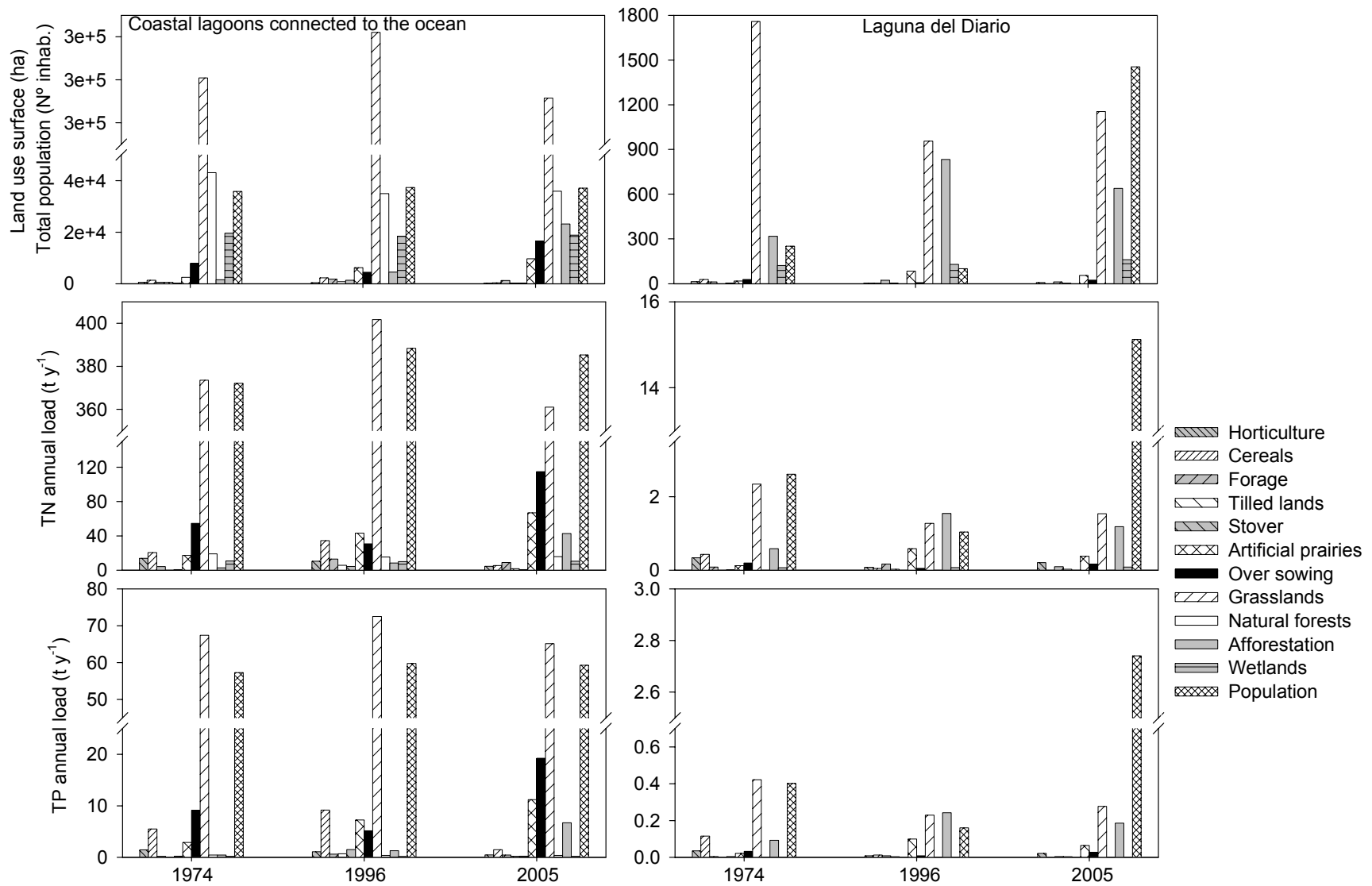


Fig. 2. Land use surface area (a and b) and total annual nutrients load (c to f) in Uruguay's coastal lagoons during the three periods studied. Data for the lagoons that still connect with the ocean were added (graphs on left) while Laguna del Diario (graphs on right) is presented separately due to the differences in land uses. Agriculture and grasslands improvement were obtained as a proportion of the "agriculture" cover in the satellite image analysis. Proportions were obtained from the corresponding National Agriculture Census. Annual loads were calculated by multiplying the surface area of each land use by specific export coefficients (see methods for a detailed explanation).

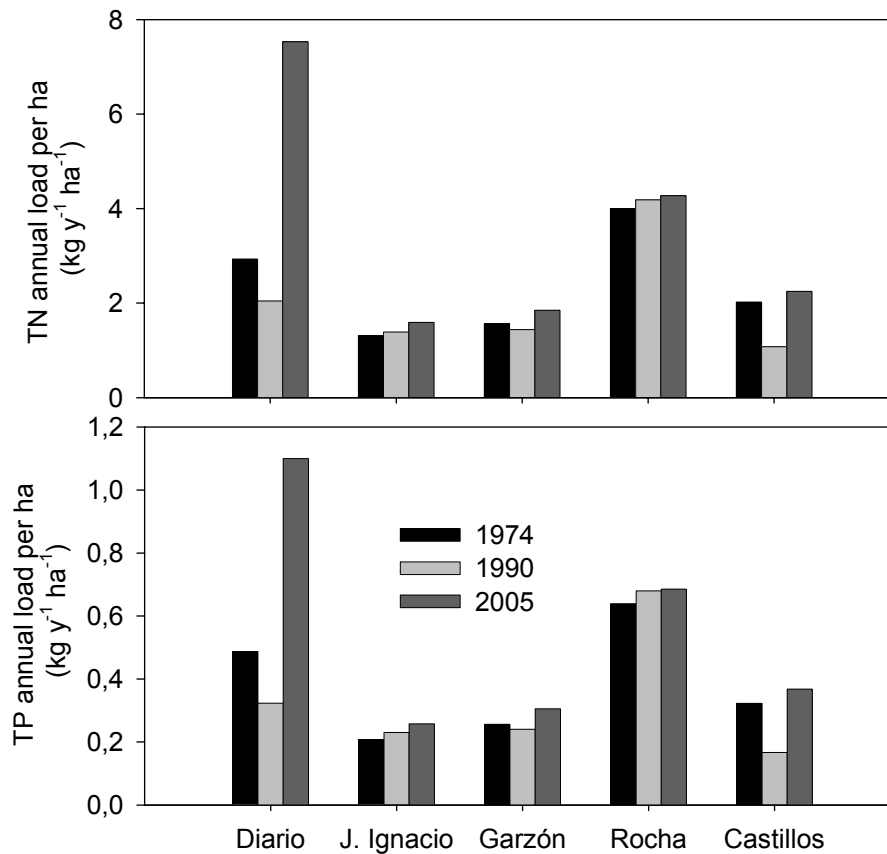


Fig. 3. Nutrients (total phosphorus and nitrogen) aerial annual load to Uruguay's coastal lagoons. Data are presented separately for each lagoon and for the three periods studied.

Relationships between land uses in the catchment area and eutrophication indicators

The significant (overall fit and slope parameter both significant) linear and non linear models among eutrophication indicators, land uses in the catchment area and soil types were 16 in 72 tested relationships (Fig. 5). Land uses and soil types were standardized by the catchment area minus the lagoons areas to remove the effect of the different lagoon and catchment surfaces areas, and therefore are unit-less. TPsed had the highest number of significant models, followed by SAV biomass. SRP, TP and phytoplankton Chl *a* were not correlated with land uses, salinity or other catchment attributes. Among the tested explanatory variables, only afforestation and agriculture had no significant models with eutrophication indicators. Phytoplankton Chl *a* and microphytobenthos Chl *a* were inversely related, but the simple correlation between them was not significant. The relationships among eutrophication indicators and explanatory variables are plotted in Figure 5. For simplicity TNsed relationships were omitted because they showed the same pattern as TPsed.

Catchment size was inversely related to most eutrophication indicators, and regressions with TPsed, SAV biomass and microphytobenthos Chl *a* were significant (Fig. 5). Eutrophication indicators generally decreased with the surface area of natural forests and significant models were found for TPsed and SAV biomass. Afforestation presented no clear relationships with the eutrophication indicators, even after removing Laguna del Diario which is the most afforested lagoon. Although agriculture exhibited no significant regressions with dependent variables, TP and microphytobenthos Chl *a* increased in lagoons with higher agriculture surface area, while DIN, TN and phytoplankton Chl *a* decreased. Eutrophication indicators increased with the wetland/lagoon ratio, with significant

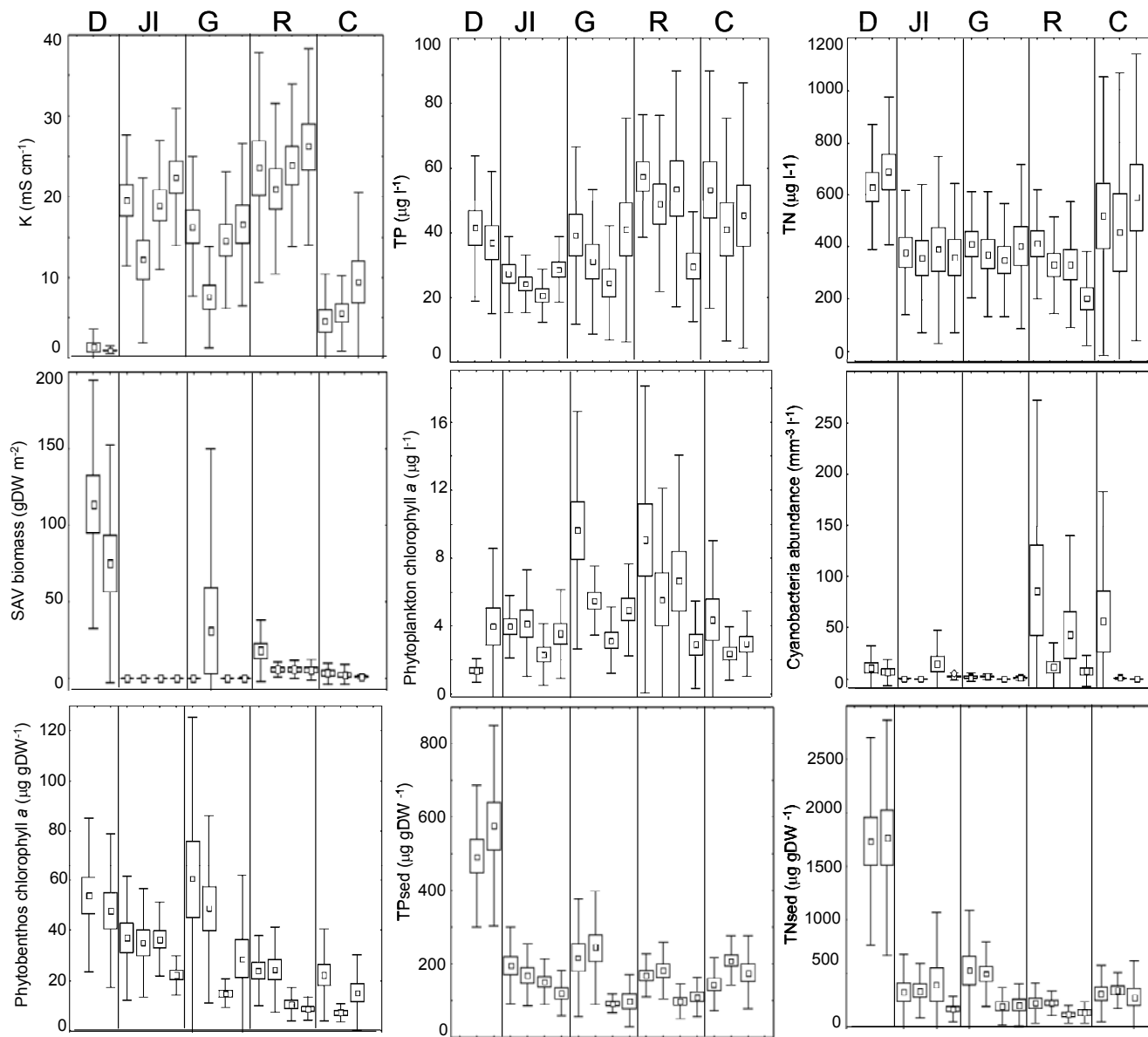


Fig. 4. Box plots of K and eutrophication indicators in all sampling points of Uruguay's coastal lagoons during 2005-2006. Mean, standard error and deviation are indicated. Lagoons are separated by lines. Sampling sites are in the following order: N and S in L. del Diario (D), NW, NE, Central and S at L. José Ignacio (JI), Garzón (G) and Rocha (R) and NW, NE and Central at L. de Castillos (C).

regressions for DIN, TN and TP_{sed}, while phytoplankton Chl *a* followed the inverse pattern. TP_{sed} and SAV biomass significantly increased with TP annual load and non-significant but also positive relationships were found for the other eutrophication indicators, except for phytoplankton Chl *a*. In general, eutrophication indicators decreased with increasing surface area of high land soils but regressions were only statistically significant for TN and TP_{sed}. On the contrary, eutrophication indicators slightly increased with soils suitable for agriculture, but only the regression with TP_{sed} was significant. SS slightly increased with catchment size, highland soils, suitable agriculture soils and was highly significant for agriculture, and decreased with natural forest area and wetlands/lagoon ratio (data not shown).

DISCUSSION

Land use change in the catchment area of Uruguay's coastal lagoons

Extensive livestock ranching (both cows and sheep) is still the dominant economic activity in Uruguay's coastal lagoon area. Cattle are only fed with natural pastures, however this traditional production system is changing and food complements such as grains, artificial prairies and grasslands improvement (natural grasslands fertilization and over-sowing) are on the rise. Artificial prairies and over sowing explain the greatest increase in the area under agriculture use observed in this study. Unfortunately, soybean expansion, which is increasing very rapidly in Uruguay (Arbeletche & Carballo 2006) was not captured in our study, because it entered the study area mainly after 2006. Therefore, new analyses may show a more intensive land use picture. The most important land use change in the 30 years study period was afforestation for wood and pulp mill production, which takes place in soils with low suitability for agriculture and livestock ranching, mainly in superficial highlands and coastal sandy soils. The species used are the exotic *Pinus* spp. and *Eucalyptus* spp. Afforestation in the catchment area of the coastal lagoons increased from 0.4% in 1974, to 1.2% during 1996 and to 6.3% during 2005 (the percentages do not take into consideration the lagoons' surface area) and is still rapidly increasing in the study area. This increase was due to the growing pulp mill and wood industry.

Our study shows that changes in land use were accelerated during the second half of the 1990s. Those changes affect 14% of the coastal lagoons catchment area and are still rapidly increasing. The ecosystem mostly affected by these changes is grasslands. By contrast, wetlands, lagoons, natural forests and sand dunes have maintained similar surface areas in time or slightly decreased. The greatest reduction in natural ecosystems was observed in sand dunes and natural forests, mainly due to the invasion of exotic vegetation in the first case and to afforestation in the second. However, in both cases higher resolution images should be used to provide an accurate quantification of the replacement rates, especially for sand dunes.

Problems other than ecosystem substitution may be also occurring. Changes in nutrient exportation from catchment areas to surface waters may have increased due to agricultural expansion. Furthermore, the distance from several agricultural fields to the shores of the lagoons decreased from 1974 to 2005. When littoral wetlands are narrow as is the case in Laguna de Rocha, artificial prairies and fertilized grasslands adjacent to the shores of the lagoons may be a major source of nutrients input during runoff events. Sharpley *et al.* (1999) found that soils with high nutrient concentration near streams have greater risks of phosphorus exportation in comparison with other soils, at the catchment scale. Moreover, these authors found that surface runoff and phosphorus loss occurred mainly from distances no greater than 60 m from the river margins. However, distance from agricultural land to surface waters in the study area are generally higher than 200 m, indicating a lower risk of nutrient exportation. Although land uses in the coastal lagoons catchment area are certainly intensifying and expanding, nutrients supplied by human settlements deserve attention too. The population in the study area is mainly concentrated in urban zones due to migration processes from rural to urban areas and to coastal resorts that are becoming permanent residential sites. This explains the population increase in the Laguna del Diario catchment area, where a completely new neighborhood was built in the last decade. In this lagoon, land uses changed from predominantly agriculture and livestock ranching to urban, since the lagoon now finds itself inserted into the

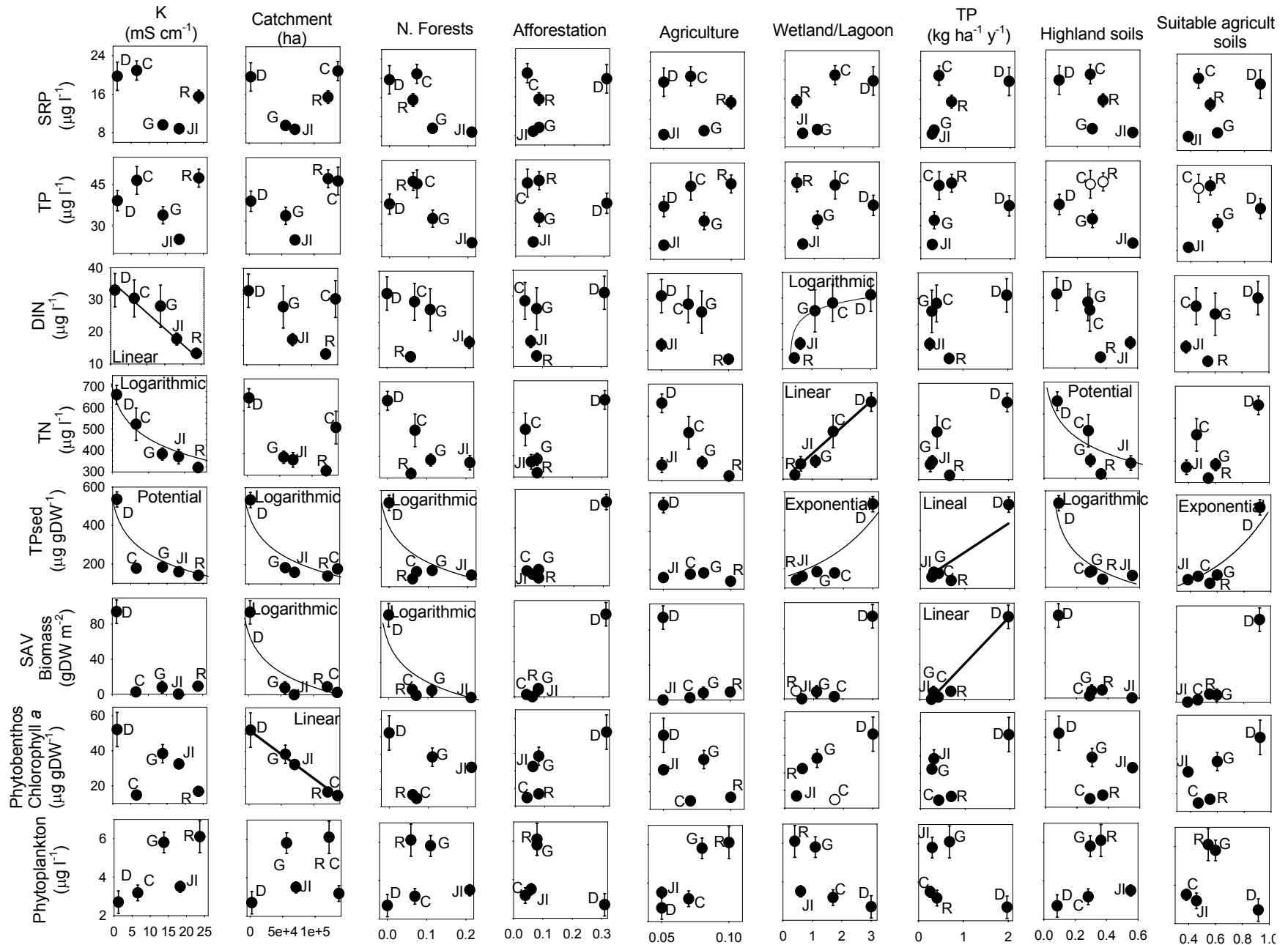


Fig. 5. Eutrophication indicators during 2005-2006 study period and their standard error plotted against explanatory variables: K, land uses and soils types. Significant models are shown. Natural forests, afforestation, agriculture, highland soils and suitable soils for agriculture were standardized by the catchment surface area, to make data comparable among lagoons. Models: Linear: $y=bx+a$; Exponential: $y=b\text{EXP}^{(xa)}$; Logarithmic: $y=b\text{Log}(x)+a$; Potential: $y=bx^a$.

Punta del Este seaside tourist area. However, total population in the other coastal lagoons was kept quite constant during the study period. In rural zones and resort villages houses only have septic tanks, while in the City of Rocha and the NE zone of Laguna del Diario, houses are connected to a sewage system. However, in the City of Rocha the sewage system does not include tertiary treatment and effluents are eventually diverted into the Rocha stream, the main tributary of Laguna de Rocha. In all cases the number of unconnected houses is high (no precise number is available).

Natural grasslands and population were the main contributors to annual nutrient load to the coastal lagoons. Grasslands are the main source of nutrients due to their large surface area, and population due to its high nutrient export coefficients. However, increases in the surface area of artificial prairies and over sowing caused the nutrient load to rise considerably in 2005. The total annual load in 2005 was 1036.1 and 167.6 t y⁻¹ for TN and TP (all coastal lagoons added), increasing 14.8% and 15.5% from 1974 to 2005, respectively. The highest aerial nutrient annual loads were observed in Laguna del Diario in 2005 and in Laguna de Rocha during the whole study period, the two most populated catchment areas. Except for Laguna del Diario, the other aerial annual loads of TP were well within the values reported for mixed agricultural catchments in the USA and lower than those reported in more intensively managed watersheds (May *et al.* 2001; and values reported therein). In all cases nutrient export to the lagoons increased slightly in the period, except in Laguna del Diario where it was triggered in 2005 at the same time as population increased. Arocena *et al.* (2000) found no effects from the sewage and runoff discharge from the City of Rocha on the water quality and benthos community in the streams that drain into Laguna de Rocha, possibly due to the riparian forests depuration effects. However, seasonal estimations of nutrient concentration in streams are not effective in capturing the nutrient loads, at least for phosphorus, since most of the sediment transport occurs during stormflow events which can account for up to 70% of the phosphorus load (Brooks *et al.* 2003). Chemical markers such as Boron (Jarvie *et al.* 2006) and biomarkers such as croptanol, among others (Nash & Halliwell 2000), should be inspected to determine if nutrient loads are derived mainly from sewage or agricultural sources.

Total nutrient load based on exportation coefficients is a gross estimation of the potential nutrient supply to surface waters (May *et al.* 2001). More detailed information on the sewage system, elaboration of specific export coefficients and modeling at the catchment scale should be conducted to obtain a more reliable picture. Most of the source soils are far away from the water bodies and transport processes may be interrupted in several places. Furthermore, in our study area soils are expected to be undersaturated of nutrients due to the low fertilization intensity, possibly increasing nutrient retention. However, this approximation may be useful in determining the most risky land uses and their spatial location. Later, a detailed analysis of nutrient export sources and risk areas *sensu* Sharpley *et al.* (2003) at a farm scale may be easily carried out and best management practices selected.

The marine influence on eutrophication indicators

The four lagoons that still connect to the ocean showed a clear decreasing salinity gradient from seaward to inward zones. The higher order streams generally discharge in the northeast of each lagoon, explaining the lower salinity values observed in these zones. Linear and non linear modeling showed that salinity was a major determinant of eutrophication indicators. Lower values of eutrophication indicators were usually found at higher salinities. This pattern was clearer for nitrogen and also for nutrients in the sediment. Organic content and nutrients in the sediments were higher in inward zones, matching decreases in granulometry. SAV and phytobenthos were more abundant towards inward zones and SAV richness also decreased towards the South. Although nutrients in the water column and phytoplankton showed larger fluctuations than the other variables, they were generally higher in inward zones. Sediment resuspension by winds in shallow coastal lagoons makes the spatial pattern noisy, because nutrients and also phytoplankton found in the water column may be alternating between water and the sediment compartments (Conde *et al.* 1999; Bonilla *et al.* 2005). Resuspension can be present during up to 13% of the annual period in Laguna de Rocha (Chalar & Clemente 2005), thus suggesting the importance of this process. Furthermore, salinity

variability superimposes a great stress on organisms, determining their composition and abundance as well. Effects of the salinity gradient have been observed in Laguna de Rocha and Castillos for phytoplankton (Bonilla *et al.* 2005), phytobenthos (Conde *et al.* 1999), bacteria (Piccini *et al.* 2006, Alonso *et al.* 2008), benthos (Pintos *et al.* 1991, Jorcín 2005), and SAV (Rodríguez-Gallego *et al.* 2010).

Strong variability of K, nutrients and Cla *a* is a common feature in coastal lagoons due to the exchange of water masses with the ocean (Flores-Verdugo *et al.* 1988; Suzuki *et al.* 1998; Medeiros-Dos Santos & Esteves 2004; Chagas & Suzuki 2005). When open to the ocean, the lagoons discharge large freshwater masses rich in sediments, nutrients and organisms. Latter, lagoons are flooded with more diluted marine waters (Kierfe 1994; Suzuki *et al.* 1998; Smakhtin 2004). Therefore, the connection with the ocean acts as a reset mechanism, removing nutrients previously transported from the catchment areas and maintaining lower nutrient concentrations. Effects of the marine intrusions on nitrogen concentration may respond to additional biogeochemical processes associated with biological denitrification promoted by SAV or interactions between water and sediments in these shallow waters and also to other sedimentary redox cycles (Mn, Fe, S) (Cornwell *et al.* 1999 and references therein). Coastal zones, including coastal lagoons usually show higher denitrification than freshwater systems (Seitzinger 1988; Nixon *et al.* 1996). Denitrification may explain the decrease of nitrate concentrations since 1981 in Laguna de Rocha (Aubriot *et al.* 2005).

On the contrary, in Laguna del Diario the natural connection with the ocean was completely modified, and therefore now lacks such a reset mechanism. As a result, accumulation of nutrients supplied from the catchment area in the sediments is strongly accelerated, enhancing internal load development. This lagoon has a stable state of clear waters dominated by SAV, phytoplankton is outcompeted and sediments are rich in organic content and nutrients (Scheffer 1998). A shift from a clear water state to one dominated by phytoplankton is a major risk due to the high nutrient content in the system (Scheffer *et al.* 2001). Moreover, even moderate harvesting may reduce the resilience of the vegetated state (van Nes *et al.* 2002). In this lagoon, the local community and public opinion influence the municipality to artificially remove plants for aesthetic and recreational reasons, especially during the summer.

Land use and the influence of soil type on eutrophication indicators

Average concentration of total nutrients and phytoplankton chlorophyll *a* in Uruguay's coastal lagoons ranged from oligotrophic to eutrophic conditions according to Håkanson (1980), OECD (1983) and Salas & Martino (1990). However, the indexes of trophic state do not include nutrients in the sediment, macrophytes or phytobenthos abundance, which are important eutrophication indicators in shallow lakes. Furthermore, some indicators may have inverse behavior at high eutrophic levels, as the phytoplankton abundance that is outcompeted by SAV (Scheffer 1998). Therefore, independent analyses of the eutrophication indicators themselves may give greater insights in shallow systems.

Eutrophication indicators tend to decrease with catchment area size. Since the size of the catchment area and the size of the coastal lagoons are strongly correlated, a dilution effect may be involved, where greater water volumes may better overcome the higher nutrient supply (Kalff 2003). Soil type may strongly determine the export of nutrients to surface waters, due to erosion potential and nutrient retention capacity. Highland soils are superficial, have relatively low fertility and are located on high slope terrains but have greater cover from natural forests. This may explain the decreasing tendency of eutrophication indicators in catchment areas where these soils are abundant. On the contrary, the eutrophication indicators increased slightly in areas with soils suitable for agriculture.

Most of the eutrophication indicators were inversely related to natural forest surface area. Therefore, highly forested catchment areas appear to export lower nutrients to the lagoons. Our findings are in agreement with other studies that found reductions in suspended solids but less clear effects on total nutrients (McKergow *et al.* 2003). Riparian forests are buffer communities that filter and decelerate the runoff due to physical effects, promoting sediment deposition before reaching the water bodies

and also uptake the groundwater nutrients (McKergow *et al.* 2003 and references therein). However, in Uruguay, cattle have access to the riparian zone along the fluvial systems, which may be lowering their buffering capacity. Cattle are attracted to riparian areas due to shade, palatable vegetation and drinking water, and therefore urine and manure are deposited in these areas, banks erode due to the reduction of herbaceous vegetation and the stream banks are also eroded. Dodds & Oakes (2006) found buffer effects on nutrient concentration in streams with 33 m-wide riparian forests. Similar widths are observed in the first and second order streams that increase downstream in our study area, indicating great buffer capacity as well. In Laguna del Diarío the buffer capacity in the catchment may be low, since the sierra and riparian forests are almost absent.

Afforestation appears not to affect eutrophication indicators, even after removing Laguna del Diarío (the most afforested catchment) from the fitted models. This can be an effect of distance, since afforestation takes place mainly in the highlands, ca. 10 km away from the lagoons' shores. Possibly, the afforestation management practices are less prone to nutrient loss, since the riparian forests are generally maintained and also tall grasses develop between the afforested trees and the riparian forests when cattle are removed during the first years of plantation. Furthermore, fertilization is conducted only for *Eucalyptus* spp. at the beginning of the plantation, which generally has a rotation of 7 to 10 years. Also, since afforestation is a recent activity effects on water quality may have not been observed yet. However the main impact of afforestation, besides natural habitat substitution, is the reduction of the annual runoff which can cause intensification of water shortages (Farley *et al.* 2005). Therefore, studies of the water balance are required to determine the impacts of afforestation on the functioning of coastal lagoons, other than the nutrient exportation rates. Conversely, in lagoons with larger agricultural areas, the total phosphorus and suspended solids increased, while, interestingly, a decrease of nitrogen was observed. The phosphorus increase may further promote a decrease in nitrogen due to a higher uptake from photosynthetically organisms that are usually co-limited by both nutrients. This co-limitation was at least found for phytoplankton in Laguna de Rocha (Bonilla 2002). Phytobenthos chlorophyll *a* tended to decrease with agriculture and phytoplankton chlorophyll *a* to increase. Dodds & Oakes (2006) did not find a relationship between agriculture area and phosphorus, but found positive relationships with nitrogen forms. These authors attributed the lack of a relationship with phosphorus to the difficulties in detecting it because of the pulse input which is generally dependent on precipitation events and on point sources. Therefore, Johnson *et al.* (1997) pointed out that phosphorus concentration may be more difficult to relate to watershed land uses. Contrary to Dodds & Oakes (2006), we found inverse effects of agriculture on nitrogen forms, which can possibly be explained by coastal denitrification. Although we found some influence of land use on nutrient concentrations in the coastal lagoons, this effect may decrease as catchments increase in size (Buck *et al.* 2004), explaining the lack of statistical significance in most of our relationships.

The ratio wetlands/lagoons surface area was significantly related to eutrophication indicators, but with an unexpected result. Generally, wetlands are considered nutrient traps, mainly in their particulate forms (Mitsch & Gosselink 2000, Vymazal 1995). However, we found increasing eutrophication indicators in lagoons with higher quotients between wetlands and lagoons surface area as Laguna del Diarío, de Castillos and Garzón. Since the largest contact area between land and the fluvial system takes place in the riparian forests, they should be playing a major role as a sink of nutrients, instead of the traditional assumption that this role is performed by wetland areas. Nevertheless, since wetlands are tightly connected to the lagoons, the linkage between these systems is strengthened during flooding events. Therefore, wetlands may be acting as sources of particulate and dissolved nutrients rather than sinks.

Despite the clear contribution of population to the annual nutrient loads, no relationship was found between population and eutrophication indicators (data not shown), even after removing the densely populated Laguna del Diarío. Possibly, the contribution of population to the annual load may be overestimated, since at least part of the Laguna del Diarío urbanization and the City of Rocha are connected to a sewage system rather than septic tanks as was considered in our evaluation.

However, although the rural population is low in comparison to urban zones (10% of the total population in the catchment area), this nutrient source should not be undervalued. Jarvie *et al.* (2006) demonstrated that the rural populations not connected to sewage systems may be a very important source of nutrients to the fluvial system. Therefore, policies to promote other forms of sewage treatment should be considered to assist the dispersed rural population.

Relationships among SRP, TP and phytoplankton chlorophyll *a* and the explanatory variables were not significant in any case and were quite erratic in many cases. These three eutrophication indicators are strongly affected by the resuspension process (Chalar & Clemente 2005), which in part explains the lack of significant regressions. In contrast, nitrogen forms and also the sediment variables were significantly related to the catchment characteristics and land uses. Stronger processes are possibly operating on those variables, resulting in clearer responses. For example for nitrogen, a strong denitrification process in the coastal lagoons may be one possible explanation, removing the external load supplied by the catchment areas. Additionally, more stable sediment conditions in comparison to the water column may explain the significant relationships between nutrients in the sediment, SAV biomass and phytobenthos chlorophyll *a*. To a lesser extent, hydrodynamics may affect the sediments, while resuspension would involve the first centimeters. Also, an insignificant but inverse relationship between phytobenthos and phytoplankton chlorophyll *a* was observed.

Management recommendations

The research approach used in this study permitted an analysis of the entire picture of nutrient export from land uses in the catchment area to Uruguay's coastal lagoons, with important research and management recommendations emerging from our results. Riparian forests in the coastal lagoons are a key conservation target due to the ecosystem buffering they provide of total and dissolved nutrients from the catchment area into the lagoons, preventing surface waters from cultural eutrophication. Native forests in Uruguay do not exceed 4% of the territory (Nebel 2004), and riparian forests represent an important proportion of it. Therefore, protecting the riparian forests to prevent eutrophication may not affect a large area but it also would contribute to biodiversity conservation. Legal protection of the natural forests already exists but needs stronger control and better enforcement. Moreover, specific management programs are required to improve their ecological integrity, since forests and understory regeneration are reduced due to cattle impacts and biological invasions. Fencing the riparian forest, at least in temporary rotation to avoid cattle access should be promoted by government policies. Also, further research and quantification is needed into the mechanisms involved in the buffer capacity of the riparian forest.

The wetlands role was not clear in this study, apparently acting as a nitrogen source of nitrogen rather than a sink. This finding demand further research and should be accompanied by hydrodynamic modeling. Furthermore, precautions should be taken when wetland are drained by land owners. Wetlands canalization may accelerate nutrient transfer to the lagoons, and also cause reductions in biodiversity. Moreover, the traditional burning of the riparian tall grasses and emergent vegetation should be controlled, not only to preserve buffer capacity but also to avoid the release of labile organic matter to the lagoons. Furthermore, the nutrient load originating from human settlements and dispersed rural population needs a more precise estimation. The input of nutrients from the sewage system is not clear, however some resorts and small fishing villages located on the shores of the lagoons undoubtedly are nutrients sources. Due to the difficulty of establishing sewage treatment works in low populated zones, national policies should promote the development of alternative systems, such as artificial wetlands (Vymazal *et al.* 1998).

The alteration of the natural connection of the lagoons to the ocean is a crucial issue, not only in order to maintain the natural functioning of these ecosystems but also to avoid eutrophication problems. The permanent interruption of Laguna del Diarío's connection with the Río de la Plata, coupled with the increase of population in the catchment area, was catastrophic for the lagoon functioning, since it drove it into a hipereutrophication process. This resulted in recreational and aesthetic drawbacks which can be considered indirect economic losses in an area close to one of the

most important South American resorts. Furthermore, the other coastal lagoons suffer artificial openings of the sand bars, conducted to avoid flooding in unplanned urbanizations and to enhance fisheries in the lagoons. The consequences of the artificial manipulations are still in need of a consistent evaluation. However, at least impacts on SAV abundance and richness were shown (Rodríguez-Gallego *et al.* 2010). The effects on hydrodynamics, sedimentation, nutrients budget and fisheries are still unknown. Nevertheless, since the connection of the lagoons with the ocean is the most outstanding feature of the natural functioning of these ecosystems, other measures such as urban planning and fisheries management should be taken to avoid flooding and enhance fisheries before altering the natural connection to the sea.

Short-term intensification of land uses is expected and climate change predictions indicate increasing precipitation and higher frequency of extreme climatic events (PNUD 2007; Bates 2008). Therefore, strategic planning processes are undoubtedly needed. Although climatic change adaptation programs do exist in Uruguay, eutrophication prevention measures and biodiversity conservation should be strengthened. Otherwise, water supply for irrigation and crop production aspects could easily dominate the management decisions. The adaptation practices to climatic change proposed for Uruguay could indeed, directly or indirectly, increase the risk of eutrophication. For example, to reduce greenhouse gasses released by cattle, the intensification of extensive livestock ranching is proposed which substitutes natural grasslands with artificial prairies, and promotes no till practices for carbon sequestration (Martino 2008). This technology may promote a higher exportation of nutrients due to the superficial concentration of fertilizers in the upper centimeters of the soil. Uruguay's coastal lagoons are protected by several national and international norms, and most of them will soon will be part of the National System of Protected Areas. However, if the ecological integrity of the coastal lagoons is to be preserved under scenarios of land use intensification, management measures must be taken beyond the park limits. Further studies are needed to confirm and quantify some of the findings obtained to date. A combination of long-term monitoring and specially designed research to elucidate certain issues is necessary.

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CAPÍTULO II: Salinity as a major driver for submersed aquatic vegetation dynamics in coastal lagoons: a mid-term analysis in the subtropical Laguna de Rocha

Lorena Rodríguez-Gallego

ABSTRACT

This paper analyzes six years of submerged aquatic vegetation (SAV) composition and abundance in the subtropical Laguna de Rocha (Uruguay) choked coastal lagoon, to explore its temporal and spatial dynamics and the main conditioning factors. We took seasonal samples of SAV biomass and physicochemical variables in vegetated areas of the entire lagoon. The spatial distribution of SAV was analyzed with Correspondence Analysis. First we selected the explanatory environmental variables that conditioned SAV abundance by a forward procedure in a Redundant Analysis, and later we used Generalized Linear Models to quantify their contribution to SAV species biomasses, total biomass and richness. Salinity was the single main conditioning factor of SAV structure, determining an increase of richness and biomass from seaward to inward zones, inverse to the salinity gradient. At salinity values higher than *ca.* 10, richness and biomass of SAV species drops sharply. The SAV temporal and spatial dynamics were also determined by the life strategies of the species. Freshwater and slightly brackish conditions allowed competitive species to develop high biomass and cover, while marine waters promoted declines in biomass and richness and stunted species dominance. The wide variation of salinity determined a highly dynamic SAV community, where SAV and also macroalgae proliferations are usually observed. Therefore, artificial openings of coastal lagoon sand bars can have strong effects on SAV. Furthermore, increases in eutrophication due to land use intensification and a rise in runoff driven by changes in precipitation might enhance SAV variability, and dominance of submerged plants, macrophytes and phytoplankton may alternate.

Key words: *Ruppia maritima*, *Zanichellia palustris*, generalized linear methods, life strategies

INTRODUCTION

Coastal lagoons are among the most productive ecosystems in the world (Knoppers 1994), sustaining important ecosystem services such as fisheries (Pauly & Yáñez-Arancibia 1994). Nevertheless, they are seriously threatened by eutrophication, pollution, urbanization, among other human impacts caused by population growth in the coastal zone (Estevez *et al.* 2008). Choked coastal lagoons are inland shallow waters periodically connected with the ocean by a narrow channel that opens through a sand barrier. These lagoons are physically dominated systems with large salinity and hydrodynamic fluctuations mainly caused by the intermittent sand barrier opening (Kjerfve 1994).

Submersed aquatic vegetation (SAV) also plays relevant structuring and functioning roles in coastal lagoons. Their contribution to primary production is especially important in lagoons with low residence time (Knoppers 1994). According to Thorne-Miller *et al.* (1983), in poorly flushed lagoons macrophytes like *Potamogeton* sp., *Ruppia* sp. and filamentous green algae might be dominant, salinity being the main selection factor. SAV can also have effects on chemical features (Rodríguez-Gallego *et al.* 2010), can prevent sediment resuspension (James *et al.* 2004), plays an important structuring role for biological communities and acts as feeding and refuge areas for crustaceans (Pérez-Castañeda & Defeo 2004) and fish (Horinouchi 2007). Also, it can exhibit attenuation effects on eutrophication, as observed in freshwater shallow lakes (Scheffer 1998). Therefore, SAV is gaining recognition worldwide due to its numerous ecosystem services (Green & Short 2003).

Understanding the factors that determine SAV temporal and spatial variability is fundamental for preserving the ecosystem services they provide and to forecast the effects of climate and land use changes. The use of functional classifications of plants based on species functional traits can help in the understanding of the response of vegetation to environmental variability and in predicting responses to environmental change, without requiring detailed information at the species level (Reich *et al.* 2003). "Strategies" are a type of functional classification that cluster species with similar adaptations to particular patterns of resource use (Lavorel *et al.* 1997). The best-known classification for terrestrial plants is the C-S-R strategies (Grime 1977) that aggregates species according to their tolerances to stress and disturbance. The Grime scheme

has been adapted to SAV by Kautsky (1988), who split stress-tolerant (S) species into "biomass storers" and "stunted", and has become a widely accepted scheme in SAV ecology (Elger *et al.* 2002). Nutrients are one of the main plant stressors (Elger *et al.* 2002) as well as salinity (Sculthorpe 1967; Touchette 2007). However, in highly fluctuating salinity systems, it is not simply salinity but also its range of variability which may act as a structuring factor for communities, as has been found for macrozoobenthos in estuaries (Attrill 2002) and exposed sandy beaches (Lercari & Defeo 2006).

Global climate change, mainly precipitation pattern changes (Bates 2008) and eutrophication processes driven by land-use intensification may also have important effects in SAV community structure. Long-term data that exceed the sub-decade scale may be helpful to reveal trends about the relative importance of natural and anthropogenic effects (Magnuson *et al.* 1991). However, long-term data are scarce in Latin American countries and in Uruguay (Conde & Sommaruga 1999). Padial *et al.* (2008) quantified the scientific publications of SAV ecology in the Neotropics and found that lake and coastal lagoon SAV is among the most frequently studied aquatic plant communities. However, as far as we know our study is one of the few which analyzes mid-term data sets for this region of the world.

Laguna de Rocha is a subtropical choked lagoon located on the Atlantic coast of Uruguay, South America. Among other relevant ecosystem services, it supports the most important inland fisheries of Uruguay's Atlantic coast (Fabiano & Santana 2006). Salinity ranges from freshwater to marine conditions due to the intermittent connection with the sea. Hydrology is the main driving force for the whole ecosystem functioning (Conde *et al.* 2000; 2002) and its effects on salinity gradients determine phytoplankton (Bonilla *et al.* 2005), phytobenthos (Conde *et al.* 1999), bacteria (Piccini *et al.* 2006), benthos (Pintos *et al.* 1991) and SAV (Rodríguez-Gallego *et al.* 2010) abundance and composition. Although confined to the shallowest littoral areas, SAV plays important ecosystem roles, acting as a trap for suspended solids and total nutrients, due to the decrease of water turbulence (Rodríguez-Gallego *et al.* 2010). Diverse and abundant macrozoobenthos assemblages (Arocena 2007), one of the key community in the energy pathway to higher trophic levels (Rodríguez-Graña *et al.* 2008), are found inside SAV patches in Laguna de Rocha. SAV is also a food resource for vulnerable aquatic birds (black necked swan and coscoroba swan) (Sarroca 2008). In tropical coastal lagoons, similar SAV biomass values to those found in Laguna de Rocha play refuge roles (Pérez-Castañeda & Defeo 2004), indicating potential effects on fisheries as well. An anthropogenic eutrophication process was indicated for Laguna de Rocha (Aubriot *et al.* 2005) and SAV proliferations observed (Rodríguez-Gallego *et al.* 2010), therefore we hypothesized an increase in SAV abundance since 2001 to 2008 promoted by nutrients increase.

This paper analyzes six years of SAV community and physicochemical variables in the subtropical Laguna de Rocha. We explore the temporal and spatial dynamics of SAV composition and abundance and evaluate the environmental factors that condition its dynamics.

METHODOLOGY

Study area

Laguna de Rocha (Rocha, Uruguay; 34° 35' S - 54° 17' W) has a surface area of 72 km² and an average depth of 0.5 m. It is a polymictic and eutrophic system (Bonilla *et al.* 2005). The North area is influenced by freshwater discharge, while the South area is influenced by the Atlantic Ocean through a channel which periodically opens through a sand bar (Pintos *et al.* 1991) (Fig. 1). This determines a steep salinity gradient decreasing from South to North, while turbidity (Conde *et al.* 2000), sediment nutrients (Rodríguez-Gallego *et al.* 2010), sediment type and organic matter (Sommaruga & Conde 1990) follow the inverse pattern. The connection with the ocean is often artificially opened by the local municipality to reduce flooding. Nevertheless, there is no long-term assessment of the impact of this hydrological modification.

Laguna de Rocha constitutes a feeding and reproductive area for important fish resources (Vizziano *et al.* 2002; Norbis & Galli 2004) and for resident and migratory aquatic birds (Aldabe *et al. in press*). Therefore, it is included in the MAB-UNESCO Reserve "Bañados del Este", was proposed as a Ramsar site and is currently being inducted into Uruguay's National System of Natural Protected Areas.

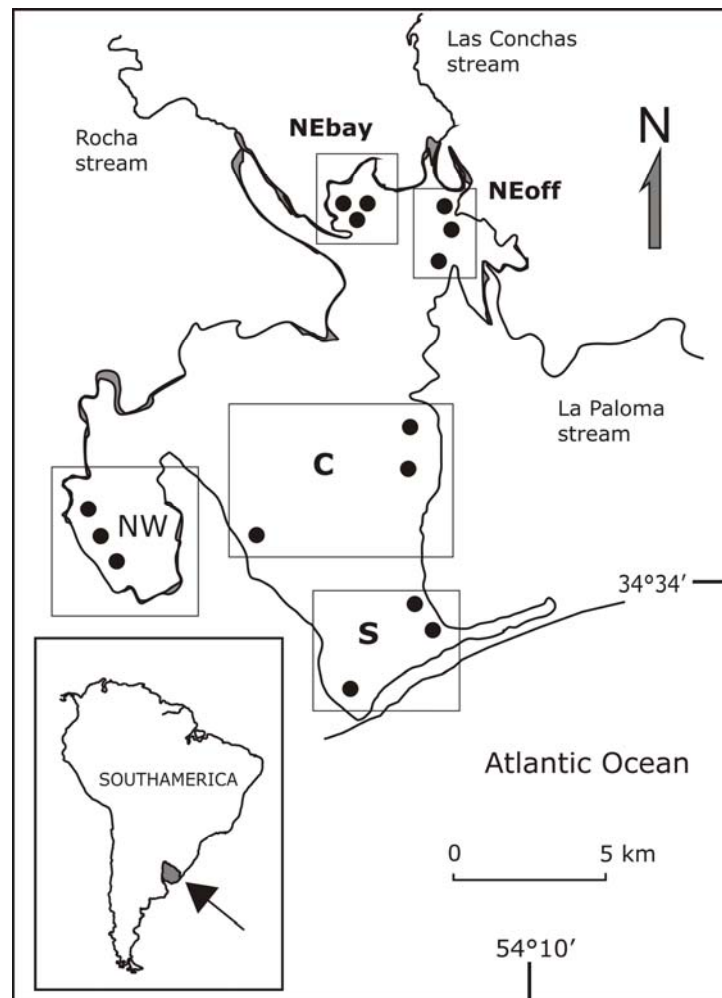


Fig. 1. Map of Laguna de Rocha, indicating the sampling zones. S: South, C: Center, NW: North West, NEbay: North East bay and NEoff: North East offshore sampling sites.

Sampling design and estimation techniques

Samples allocation intended to capture the entire salinity gradient as well as the influence of the main tributaries. We conducted all samplings in vegetated areas in three sites of the lagoon: South and Center (SC), North West (NW), and North East (NE) (Fig. 1). In NE we discriminated the small bays (NEBay) from offshore vegetated zones (NEoff), because of a higher spatial heterogeneity in the latter (Rodríguez-Gallego *et al.* 2010) (Table 1).

A total of 21 samplings of SAV biomass were conducted seasonally between 2001 and 2008, with 18 of them including physicochemical data. Gaps in monitoring occurred in autumn 2001 and throughout 2002 and 2007, while in 2008 only a spring sampling was conducted. Also, the spatial effort of sampling was not uniform: NEBay was sampled from 2001 to 2004, NEoff from 2003 to 2008, CS from 2005 to 2006 and S from 2003 to 2008.

We collected SAV biomass with an Ekman grab in three random replicates in each site. SAV biomass was sorted by taxa and dry weight was estimated after 48 h at 80 °C. Charophytes and

Non-Charophytes algae species were not discriminated into species. Total SAV biomass (TB) was calculated as the sum of individual species biomass. *In situ* variables were also measured by triplicate with field equipment, in the same sampling points as SAV. The included variables were: depth, pH, temperature, dissolved oxygen, conductivity (K as an estimator of salinity), and photosynthetically available radiation (PAR, to derive PAR attenuation coefficients K_d PAR). Salinity was derived from conductivity using a conversion factor of 0.6 (Margaleff 1983). The Venice system (1959) was used for the classification of waters according to salinity.

Water samples were collected at ca. 10 cm depth with a Ruttner bottle, after verifying that the water column mixed completely by checking temperature and conductivity every 20 cm. We later analyzed total suspended solids (SS; APHA, 1985), ammonium (NH₄; Koroleff, 1970), nitrite (NO₂; Strickland & Parsons, 1972), nitrate (NO₃; Mackereth *et al.*, 1978), total nitrogen (TN; Mackereth *et al.*, 1978), soluble reactive phosphorus (SRP; Murphy & Riley, 1962), total phosphorus (TP; Valderrama, 1981) and reactive silica (RS; Mullin & Riley, 1955). Dissolved inorganic nitrogen (DIN) was estimated as the sum of NH₄, NO₂ and NO₃ forms. Sediment samples were manually collected down to a depth of 2 cm using acrylic corers (5 cm in diameter). The organic content of the sediment was determined by ignition (OMsed; APHA, 1985) and TN (TNsed) and TP (TPsed) according to Valderrama (1981). Precipitation and air temperature data were obtained from Rocha's National Meteorological Service Station. The sand bar state (open or closed) was visually inspected during each sampling.

Data analyses

We explored the spatial distribution of the SAV species biomass and selected the main controlling environmental variables with ordination methods. A preliminary Detrended Correspondence Analysis with log₁₀ +10 transformed biological data was conducted to select the type of ordination method. Unimodal response models (Correspondence Analysis - CA) were selected when gradient lengths were higher than two, while in the inverse case linear models (Redundant Analysis- RDA) were used (ter Braak & Smilauer 1998).

We conducted a sequence of CAs with SAV biomass discriminated by species to analyze their zoning in the lagoon, using all replicates (number of cases = 193). Non-Charophytes algae were removed because they represented outliers. Differences between groups of samples were statistically tested with a Mann-Whitney U test. We classified the vegetated zones in freshwater, brackish and marine according to the Remane diagram of organism distribution in the salinity gradient (Remane & Schlieper 1971).

We used RDA to select the environmental variables that explained the SAV species biomass temporal and spatial variability, using samplings where both SAV and physicochemical data were available. Replicates were averaged since SAV and physicochemical data sets did not match exactly due to different efforts in data collection (number of cases = 58). We assessed the importance of each explanatory variable using the forward selection procedure in a RDA and only included variables with a significant ($p < 0.05$) contribution. Afterwards, we inspected the variance inflation factors (VIF) and removed variables with values higher than 20 (ter Braak 1986). Therefore, we retained a smaller number of environmental variables with high-explained variance and low redundancy. In addition Spearman correlations (r_s) were used to evaluate linear relationships among SAV species biomasses and environmental variables.

To quantify the contribution of selected environmental predictors of species biomass, TB and SAV richness, we used Generalized Linear Models (GLZ). We selected this analysis due to its robustness when the normality assumption is not fulfilled (McCullagh & Nelder 1989). Gamma and Poisson distributions were assumed for SAV biomasses and richness, respectively, while the link function was log in all cases. We used the Akaike Information Criteria (AIC) to select the best models. Following Burnham & Anderson (2002), the models retained were those with the highest AIC and a difference with other models with lower AIC smaller than 2 ($\Delta < 2$). Also, when the parameters of the variables included in the models were not significant the model was discarded.

For SAV richness we used the Pearson χ^2 to estimate the overdispersion parameter, which is recommended when variables are not continuous (Burnham & Anderson 2002). TB had to be log-transformed to improve residuals distribution that was inspected according to McCullagh & Nelder (1989). Also, a multiple regression was conducted using salinity and the first axis of a PCA (Principal Component Analysis) as predictors, along with the rest of selected explanatory variables. According to McCullagh & Nelder (1989) we estimated the goodness of fit by the deviance, and when the ratio deviance/degree of freedom was higher than 1, the models were discarded. The significance of the parameters estimates were tested with the Wald Statistic. Finally, equations were fitted to relate salinity with TB and richness.

RESULTS

The SAV community in Laguna de Rocha

SAV richness and biomass increased from South to North (Table 1 and Fig. 2). SAV was absent only in 8.1% of the samples, mainly those near the channel that opens through the sand bar. The community was composed by eight taxa (Table 1), including six vascular plants, two Charophytes (*Chara* sp. and *Nytella* sp.) and at least three taxa of Non-Charophytes macroalgae (*Cladophora* spp., *Aphanotece* sp. and *Enteromorpha* sp.), which formed dense mats above plants and sediments.

Biomass was strongly and positively correlated with SAV species ($r_s > 0.723$, $p < 0.001$ in all cases). *Myriophyllum quitense* and *Eleocharis* sp. were the two main species contributing to TB (Table 1), achieving maximum biomass values of 254.4 and 223 g DW m⁻², respectively. However, these species were restricted to NEBay and NW sites. *Ruppia maritima* was the most frequent species (73% of the samples) and was distributed along the entire system, being dominant in most samples mainly on the SC sites. Charophytes, *Z. palustris* and *P. pectinatus* presented intermediate frequency (37.8 to 44.0% of the samples) and low biomass (Table 1). The first two were distributed in the whole lagoon, while *P. pectinatus* was absent in the southernmost sites. *Potamogeton pusillus* was the rarest species and was recorded only in NEoff and NEBay with low biomass (Table 1). *Cladophora* sp. was observed only in NEBay, *Enteromorpha* sp. mainly in NW and *Aphanotece* sp. both in northern and southern stations (data not shown). The biomass of the Non-Charophytes algae achieved a maximum value of 131 g DW m⁻², with *Aphanotece* sp. being the dominant taxa.

Table 1. Mean and standard deviation (in brackets) of SAV species biomass (g DW m⁻²), total biomass and SAV richness in the sampling sites of Laguna de Rocha during the study period. Total number of samples = 210.

	SC	NW	NEoff	NEBay
<i>Ruppia maritima</i> L.	4.6 (6.9)	2.2 (2.6)	7.6 (16.3)	4.4 (11.0)
<i>Zanichelia palustris</i> L.	0.9 (2.0)	0.6 (1.4)	1.0 (3.4)	1.5 (5.7)
<i>Potamogeton pectinatus</i> L.	0.1 (0.9)	0.5 (0.9)	9.2 (22.3)	3.7 (8.2)
<i>P. pusillus</i> L.	0.0 (0.0)	0.0 (0.0)	0.7 (4.0)	0.9 (2.9)
<i>Eleocharis</i> sp. <i>nana</i> aff.	0.0 (0.0)	0.2 (0.9)	0.3 (1.2)	54.3 (58.5)
<i>Myriophyllum quitense</i> HBK	0.0 (0.0)	7.9 (18.6)	0.9 (3.9)	26.2 (44.1)
Charophytes	0.0 (0.2)	0.4 (0.5)	0.5 (1.0)	9.4 (27.4)
Non-Charophyte algae	0.1 (0.7)	3.0 (8.4)	3.1 (18.7)	1.3 (7.0)
TB (g DW m ⁻²)	5.8 (7.6)	14.7 (18.5)	23.3 (38.9)	101.6 (86.8)
SAV richness	1.3 (1.0)	2.8 (1.5)	2.9 (1.3)	4.1 1.1

Temporal patterns of SAV biomass

In the NE Bay zone SAV biomass increased during warmer months (Fig 2B). However, a seasonality pattern was not observed in the other zones of the lagoon (Fig 2C). During summer 2003 a SAV proliferation event was observed (Fig 2C), reaching the maximum biomass values for most species (species data are not shown). *Potamogeton pectinatus* was the main species responsible for this major change, achieving a maximum value of 126.2 g DW m⁻². Unfortunately, no data for the NW site was available at that moment. A sudden biomass decrease in the system (data for NE Bay are not available) was registered in spring 2005 (Fig. 2C) and *M. quitense* was the most affected (species data are not shown). Salinity was generally lower until winter 2005, increasing afterwards in the entire lagoon (Fig 2A).

Species spatial distribution

The CA conducted to analyze the spatial distribution of SAV species discriminated three vegetated zones along a gradient of increasing richness from South to North (Fig. 3). This analysis explained 82.2% of the species variance, and the three zones showed significant differences in species biomass (Mann-Whitney Zadj > 4.9, p < 0.001, for all paired comparisons). A seaward zone included samples of the SC sites, a middle one comprised mainly NEoff and NW samples and also those of other sites, while an inward zone included mostly NEBay samples.

The first two zones included samples with a large range of biomass. Samples dominated by *Z. palustris* showed the lowest biomass, while biomass was higher when *R. maritima* dominated. The inward zone was dominated by *Eleocharis* sp. and *M. quitense*, but Charophytes were also abundant and *P. pusillus* was occasionally recorded. This zone showed the highest richness (all taxa were present) and shared the maximum TB with some samples from the middle zone. The middle zone showed an intermediate behavior between the other two, and *P. pectinatus* was frequently found with higher abundance.

Environmental dynamics

Daily mean air temperature during 2001 to 2006 ranged from 10.3 to 23.5 °C, while annual average precipitation was 1366 mm and did not show any seasonal pattern. The sand bar was open during half of the samplings. It was closed most of the summers and open most of the autumns. Water depth ranged from 0.3 to 2.0 m, with a mean value of 0.6 m. Polymixis and saturation of dissolved oxygen was always registered and pH was close to neutral (7.7 ± 0.4).

Salinity ranged from a minimum of 0.1 to a maximum of 51.5 which represents a range from freshwater to marine conditions, respectively. A clear gradient was observed, where salinity decreased from South to North (Table 2). The inward zone was always freshwater (0.5 to 10.7). The middle zone was predominantly brackish and showed the widest salinity variation (0.1 to 51.5), ranging from freshwater to marine. The seaward zone also ranged from brackish to quasi-marine (Table 2, Fig. 3B) but with a lower salinity variation (9.5 to 47.7).

Contrary to salinity, RS, dissolved and total nutrients were higher in the inward zone (Table 2). Generally, nutrients in water and sediments were significantly and negative correlated with salinity (rs = -0.71, p < 0.001 with RS; rs = -0.40, p < 0.001 with TP). NH₄ and NO₃ forms contributed equally to DIN, while NO₂ concentration was always very low (data not shown). TNsed, TPsed and OMsed also increased northwards, and achieved maximum values in the NEBays and the semi-enclosed NW site (Table 2). OMsed and nutrient concentration in the sediments were highly correlated (rs > 0.55, p < 0.001).

Kd was highest in the NW and lowest at the SC sites (Table 2). It was positively correlated with SS (rs = 0.63, p < 0.001). Light at the bottom showed an inverse pattern to Kd (rs = -0.85, p < 0.001), decreasing with Z (rs = -0.48, p < 0.001) and SS (rs = -0.52, p < 0.001). Additionally, 25% of the samplings showed values of light at the bottom lower than 5%, mainly at northern stations, but also in several SC samplings.

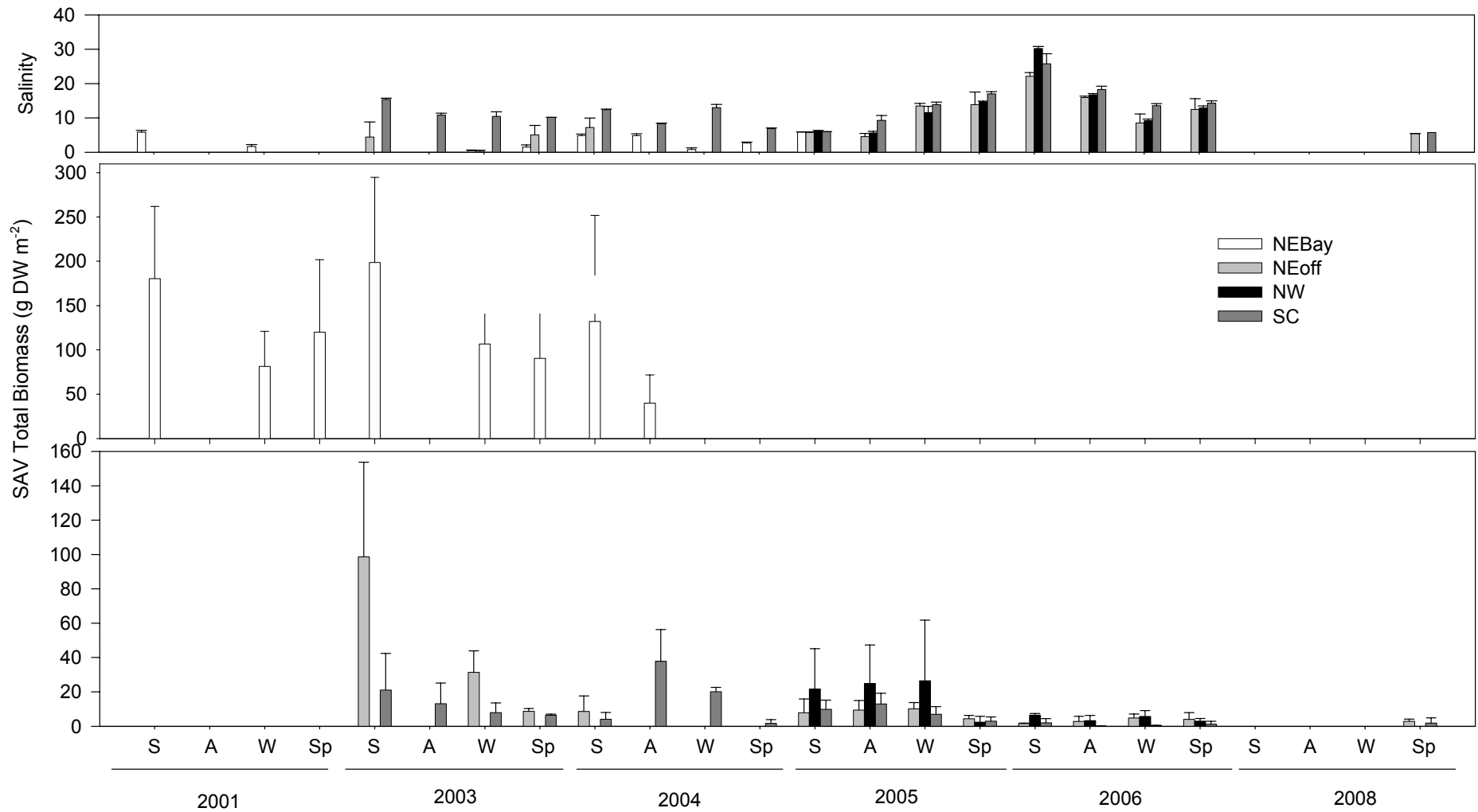


Fig. 2. Mean and standard error of salinity and SAV total biomass in the four vegetated zones in Laguna de Rocha during the study period. a) salinity; b) SAV total biomass in the Bay and c) SAV total biomass in NEoff, NW and SC sites. Absence of bars indicates lack of data. S: summer, W: winter, Sp: spring, A: Autumn. Total number of samples = 210.

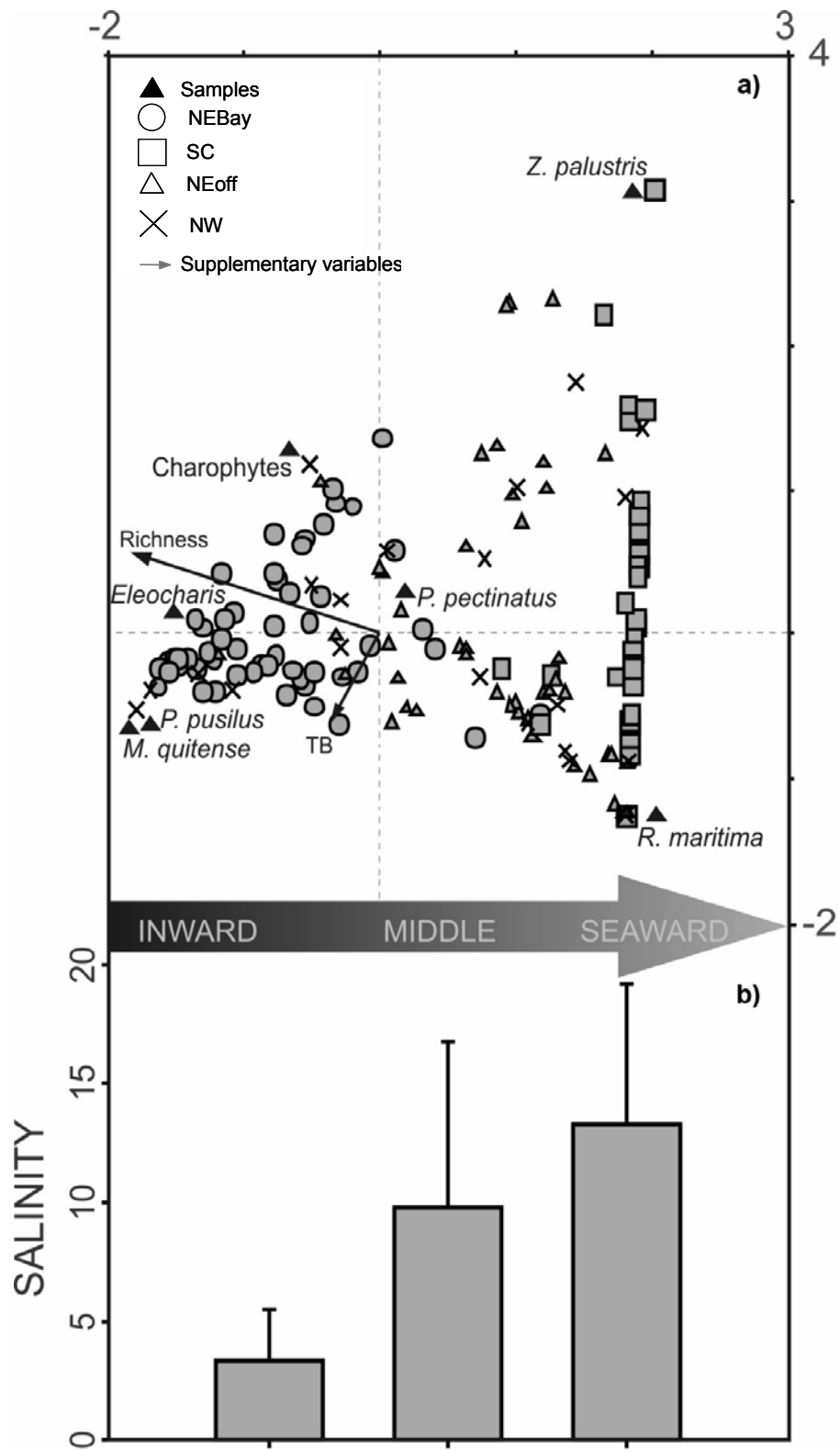


Fig. 3. a) Correspondence Analysis (CA) biplot of SAV species biomass. All samplings and replicates were included. Richness and total biomass (TB) were added as supplementary variables to the diagram (arrows). b) Mean and standard deviation of salinity of all samples in the inward, middle and seaward zones identified by the CA.

SAV structure and physicochemical variables

Generally, SAV species were associated with high concentrations of nutrients in water and sediments and OMsed. *Eleocharis* sp., *M. quitense*, Charophytes, *P. pectinatus* and *P. pusillus* correlated with OMsed (r_s from 0.49 to 0.32, $p < 0.001$) and with RS (r_s from 0.50 to 0.32, $p < 0.001$). Correlations with NTsed, TP and TN were frequently significant and positive but had low Spearman coefficients. The exceptions were *Z. palustris*, *R. maritima* and Non-Charophyte algae that were slightly negative related to nutrients or showed no significant correlation. Most species were negatively influenced by salinity (r_s from -0.56 to -0.42, $p < 0.001$), while Charophytes were slightly affected ($r_s = -0.25$, $p < 0.001$). In contrast, *R. maritima*, *Z. palustris* and Non-Charophytes algae showed no significant correlation with salinity.

The environmental variables selected by the forward procedure in a RDA (analysis omitted) containing all species biomass were: salinity, Kd, PRS, RS, TNsed, OMsed and light in the bottom. These explanatory variables were offered to the GLZ to determine their effects on SAV species biomass, TB and richness. We did not obtain significant regressions for the individual SAV species

Table 2. Mean and standard deviation (in brackets) of water and sediment physicochemical variables in the sampling sites of Laguna de Rocha for the whole sampling period. Acronyms are explained in the methodology section. Total number of samples = 168.

	SC	NW	NEoff	NEBay
Z (m)	0.67 (0.4)	0.4 (0.2)	0.6 (0.3)	0.6 (0.3)
Salinity	13.50 (5.94)	13.38 (7.50)	8.04 (6.06)	3.72 (2.46)
Kd (m^{-1})	2.3 (2.4)	5.7 (2.9)	3.3 (2.6)	3.0 (1.4)
Lz (%)	42.6 (26.9)	18.1 (18.5)	25.3 (18.)	19.9 (17.8)
SRP ($\mu g l^{-1}$)	12.3 (10.8)	12.0 (11.7)	22.3 (39.0)	16.8 (10.7)
TP ($\mu g l^{-1}$)	66.2 (84.8)	55.3 (17.8)	146.4 (255.4)	132.2 (184.4)
DIN ($\mu g l^{-1}$)	16.9 (17.9)	17.9 (18.3)	21.8 (19.4)	30.9 (31.3)
TN ($\mu g l^{-1}$)	355.7 (278.2)	444.7 (236.0)	545.5 (378.0)	728.8 (572.2)
RS ($\mu g l^{-1}$)	1368 (914.4)	1527 (1169)	2377 (1087)	3144 (788.1)
SS ($mg l^{-1}$)	39.3 (41.2)	85.4 (51.7)	52.3 (46.2)	43.0 (25.9)
OMsed (%)	1.1 (1.1)	2.9 (2.1)	1.8 (1.2)	15.9 (8.6)
TPsed ($\mu g P g^{-1} PS$)	92.0 (51.9)	189.6 (89.3)	147.4 (87.6)	229.1 (376.6)
TNsed ($\mu g P g^{-1} PS$)	120.2 (95.7)	250.3 (175.8)	214.0 (197.6)	518.0 (886.3)

biomasses (Deviance/Degree of freedom $\gg 1$), however we did find a significant result for richness and TB. Both richness and TB had a clear negative relationship with salinity (Table 3). In the case of richness, only one regression model was significant and salinity was the unique predictor (Table 3). For TB two regression models were selected, one containing salinity as the unique predictor and another one with salinity and OMsed. In both models salinity showed a negative effect on TB, while OMsed had a positive one. The GLZ conducted with salinity and the first axis of the PCA containing the other predictors was only significant for TB, again salinity had a negative effect and the first axis of the PCA a positive one (Table 3).

The particular effect of salinity on SAV

Since salinity was the single variable most selected by the multiple linear regression analyses, simple regression curves were fitted between salinity and SAV richness and TB. Both richness and TB showed a significant potential decay with salinity, decaying towards higher values ($r = 0.41$, $F = 121.0$, $p < 0.001$ and $r = 0.48$, $F = 21.6$, $p < 0.001$, respectively, see Fig. 4).

Table 3. Generalized regression models for SAV richness and total biomass as dependent variables and physicochemical variables as predictors. The Best model procedure with the AIC criteria was used and only the models with significant parameters for all predictors were retained. A regression with salinity and the first axis of a PCA performed with the predictors was also included. Replicates were averaged and samplings with no environmental data were excluded. Statistical details are indicated in the Methods section, as well as acronyms. The table includes the best models (ordered by increasing AIC values), their corresponding AIC and p values, the significant estimates of the predictors and the corresponding Wald statistic, the Desviance, Pearson χ^2 and DF of each model.

	Best models	AIC	p value	Significant parameters estimates	Wald Statistic	Desviance	Pearson χ^2	DF
Richness	Salinity	106.4	< 0.001	Intecept = 1.37 Salinity = -0.03	77.35 10.54	18.2	18.2	46
TB	Salinity	52.9	< 0.001	Intecept = 0.35 Salinity = -0.02	5.94 7.82	14.86	50.34	46
	Salinity OMsed	53.8	< 0.001	Salinity = - 0.02 OMsed = 0.15	5.74 4.74	13.65	49.16	44
	Salinity first axis PCA			Intecept = 0.34 Salinity = - 0.02 Firs axis = 0.0056	6.13 13.34 6.4	13.10		45

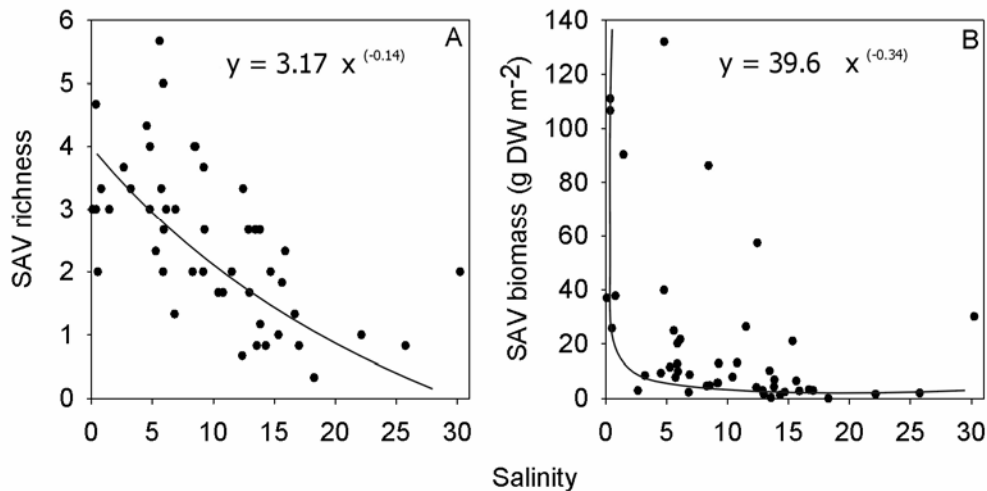


Fig. 4. Best models fitted between salinity and SAV richness (A) and total biomass (B) in Laguna de Rocha during the study period. Average of replicates was used as input data to diminish dispersion. A potential model was significantly fitted for SAV richness and total biomass.

Despite the clear effect of salinity on TB, the different species showed very different tolerance to the salinity gradient. *Potamogeton pusillus* did not tolerate brackish conditions, while *Eleocharis* sp., *M. quitense* and Charophytes tolerated from freshwater to brackish conditions (0.06 to 12.00) but biomass peaked in freshwater. *Potamogeton pectinatus* occurred in freshwater and slightly marine conditions (0.06 to 16.80) but its highest biomass was observed in brackish waters. *R. maritima* and *Z. palustris* showed the greatest salinity tolerance (0.1 to 51.5 and 0.1 to 47.7, respectively). However, both species presented their maximum biomass in freshwater, while *R. maritima* exhibited a secondary biomass peak in the limit between brackish and marine water. Non-Charophytes algae were absent in freshwater, but preferred brackish conditions (Fig. 5).

The maximum biomass of all species was recorded in inward zones and intermediate brackish conditions (0.06 to 12.00). In middle zones, after a salinity of value of 10 maximum biomass and also richness dropped rapidly (Fig. 5), In middle zones when salinity is above 25 and in seaward zones only *R. maritima*, *Z. palustris* and Non-Charophytes algae occurs, but with low biomass. A salinity value of around 5 to 10 seems to be the tolerance threshold for the whole SAV community biomass and richness; above that threshold richness and biomass decreased very rapidly (Figs. 4 and 5).

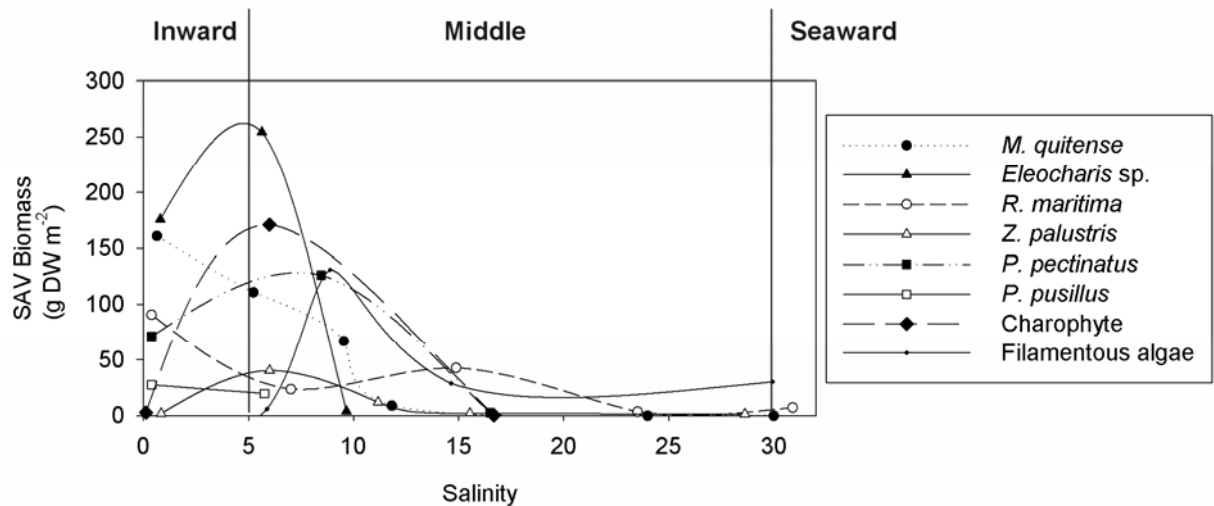


Fig. 5. Maximum species biomass (gDW m⁻²) under freshwater, brackish and marine conditions in Laguna de Rocha during the study period. Inward, middle and seaward zones are indicated.

DISCUSSION

The SAV community

SAV in Laguna de Rocha was composed of the typical association of taxa of other brackish systems (Kautsky 1988; Kantrud 1991), although we found higher species richness of salinity-tolerant submersed plants (excluding Non-Charophyte algae) than in other Uruguayan (Bonilla *et al.* 2006) and regional (Seeliger 1998; Bortolus *et al.* 1998) choked coastal lagoons. Species richness could be even higher if the taxonomic resolution of Charophytes is improved. Alternating salinity ranges might reduce the dominance of few species, allowing coexistence of freshwater and marine taxa, thus increasing richness (Estevez *et al.* 2008 and references therein). However, the richness of Non-Charophyte macroalgae was low, contrasting with Lagoa dos Patos (Selliger 1998) and other coastal lagoons worldwide (Fox *et al.* 2008; Mouillot *et al.* 2005).

SAV was present all year round, composing a quasi-continuous belt along the shores. This fact is not commonly observed in other coastal lagoons in Uruguay. In Lagoa dos Patos (Brazil), *R. maritima* is also present most of the year (Seeliger 1998), which is not the case in Mar Chiquita

(Argentina) (Bortolus *et al.* 1998). However, in both lagoons biomass is usually greater than in Laguna de Rocha. We found seasonal fluctuations of SAV in inward zones of Laguna de Rocha, coinciding with Arocena's (2007) findings. However, seasonality was not observed in middle and seaward zones. Salinity variations may mask seasonal patterns in choked coastal lagoons, especially when the connection with the ocean is not only determined by seasonality.

Salinity is the main structuring factor for SAV development

Salinity was the most important environmental variable in determining the SAV community in the choked Laguna de Rocha. The generalized regression models selected salinity as the single factor affecting species richness and it was also the most important for SAV TB. Both biomass and richness dropped sharply above salinity values of ca. 10. Salinity is one of the major determinants of plant composition and abundance (Sculthorpe 1967; Touchette 2007). In this lagoon, most species grew better in freshwater or slightly brackish conditions, according to their tolerances. *Potamogeton pusillus* is a strictly freshwater species (Schütz Rodrigues & Irgang 2001) and therefore was the most affected by salinity increase. *Eleocharis* sp. (no ecological information for this taxa is available) and *M. quitense* have moderate tolerances to salinity (Orchard 1981). Charophytes (Graham & Wilcox 2000) and *P. pectinatus* (Kantrud 1990) tolerates brackish conditions well while the Non-Charophytes algae *Aphanotece* sp. aff. *salina* and *Enteromorpha* sp. are both tolerant to salinity (Komárek & Anagnostidis 1999; John & Sheath 2003). Nevertheless, even the taxa most tolerant to salinity, *Z. palustris*, Non-Charophyte algae and *R. maritima*, preferred brackish waters. We found *Z. palustris* tolerating higher salinity values than those reported by Kautsky (1991), while *Ruppia maritima* which is the angiosperm with the highest tolerance to salinity fluctuations (Kantrud 1991) can also be stressed in both extremes of the gradient (Murphy *et al.* 2003). Therefore, the frequent and steep salinity changes in choked coastal lagoons determine SAV zoning, composition and abundance, affecting even the most salinity tolerant species.

Although salinity was the most important variable affecting the SAV community, the generalized regression models selected the content of organic matter of the sediment as an additional factor that positively affects SAV total biomass. Also, the generalized regression conducted with salinity and the first axis of a PCA with the other environmental predictors was also significant and positively related to SAV total biomass. These results indicate that other factors might be important as well. Therefore, the relationship between SAV and resources were not clear, and studies specifically designed to evaluate nutrients and light limitation in SAV beds should be conducted in this lagoon.

Can life strategies explain SAV community dynamics?

Salinity fluctuations may also act as a disturbance factor since rapid salinity changes can promote massive decreases of SAV. Attrill (2002) found that in estuaries the variability of the salinity explained the macrozoobenthos distribution better than salinity itself. Therefore, adapting the square scheme of species strategies proposed by Kautsky (1988) to choked coastal lagoons, salinity may contribute to habitat favorableness while salinity fluctuation contributes to habitat unpredictability.

Under stable environmental conditions, competition between species might occur and high biomass species can dominate the community (Herbert *et al.* 2004). Inward freshwater zones in Laguna de Rocha may be acting as a C selective environment, with low stress and disturbance. Most species find optimum conditions for growth in this zone, explaining the higher richness and biomass, and the dominance of C species such as *M. quitense* and *Eleocharis* sp. *Myriophyllum quitense* has typical attributes of C species, developing dense canopies that emerge out of the surface (Orchard 1981), coinciding with Kautsky (1988) classification of *M. spicatum*. We considered *Eleocharis* sp. a C strategist because it forms dense mats close to the sediment, has high biomass production and low tolerance to salinity. Also Charophytes prefer freshwater, but their low biomass in most samplings indicates that other species may outcompete them in the inward zone. *Potamogeton pectinatus* behaved as C-B strategy *sensu* Kautsky (1988), since it

grew better in brackish and more unpredictable middle zones, avoiding competition with the C species in inward zones. On the contrary, seaward zones are less favorable and predictable, due to higher salinity and salinity variations, respectively. Therefore, the C and C-B species cannot grow and a very stable community mainly of S species develops, but with lower richness and biomass than in middle and inward zones.

Considering salinity as a stress and salinity variations as a disturbance factor in Laguna de Rocha, *R. maritima* and *Z. palustris* were classified as S, since they were perennial and sexual reproduction was rarely found. In contrast, Kautsky (1988) considered them as R, where they showed short periods of rapid growth. This coincides with Kanthrud (1990 and references therein), because *R. maritima* can alternatively behave as annual (prevalence of sexual reproduction) in disturbed environments or as perennial (mainly vegetative growth) in stable and more saline environments. The lack of B and R species could be explained by the absence of appropriate habitat. B species would be favored by high and stable salinities, conditions unfeasible to develop due to the intermittent connection of the lagoon with the ocean. On the contrary, R species favoring habitat was probably not represented by our sampling design. Stream outlets could probably be considered R selective habitats, where favorable freshwater conditions would prevail, but stream discharge quite frequently remove biomass.

The macrophytes life strategies are also a response of the community to the wide salinity variability of Laguna de Rocha, explaining SAV dynamics and driving permanent re-colonizing and retracting of species. Nevertheless, biomass and cover is maintained all year round by an alternation of life strategies. SAV species are always "ever ready" to colonize (*sensu* Barrat-Segretain & Bornett 2000), under freshwater and slightly brackish conditions C and C-B species can colonize larger areas of the inward and middle zones, until other factors become stressors (e.g. turbulence promoted by wind). During this phase, maximal biomass is achieved because the C and C-B species are typically high biomass producers (Grime 1977; Kautsky 1988). After marine intrusions, non-tolerant species retract to "refuge areas" (*sensu* Barrat-Segretain & Bornett 2000) with lower salinity fluctuations, where they maintain viable populations. Conversely, S and S-B species persist in the entire system with lower biomass but without major effects of salinity. The colonization and retraction of SAV can be a fast process in Laguna de Rocha, as it was described by Rodriguez-Gallego *et al.* (2010). During summer 2003, an extensive SAV ephemeral proliferation was developed, possibly due to a long period of isolation of the lagoon from the ocean and therefore freshwater conditions prevailed. During fall, the artificial opening of the sand bar caused a sudden salinity increase that promoted a massive decrease in SAV cover and biomass. A similar phenomenon was also observed in the NW sampling site, where *M. quitense* decreased drastically after winter 2005, coinciding with an increase in salinity.

The persistence of C and C-B species in the refuge areas is possibly enhanced by seed and propagule banks in the sediment. In highly variable estuaries seed reserves may be responsible for the persistence of the whole community (Riddin & Adams 2009). *Myriophyllum quitense* may have an important seed and propagule bank since it had abundant flowers and strong rhizomes, while tubers of *P. pectinatus* were frequently found, which is the main strategy for re-establishment of the species (Kautsky 1987). *Eleocharis* sp. has abundant rhizomes and the whole plant can float after dislodgements caused by turbulence, thus being transported long distances. On the contrary, *R. maritima*, which performs well through vegetative propagation (Kanthrud 1991), as well as *Z. palustris* and Charophytes, were rarely found in sexual reproduction. Therefore, the SAV community in choked coastal lagoons develops strategies to overcome natural salinity variations and to maintain biomass and richness throughout the year.

Development of SAV under diverse scenarios

Phosphorus enrichment seems to be occurring in Laguna de Rocha (Aubriot *et al.* 2005), possibly due to land-use intensification in its catchment area and sewage discharge. The increase in precipitation and runoff (Genta *et al.* 1998; Bates 2008) could amplify nutrient input and trigger an increase of SAV biomass and cover. On the contrary, denitrification processes may be

explaining the nitrate decrease in the same lagoon (Aubriot *et al.* 2005). We did not find any consistent trend of SAV biomass increase or decrease, but rather a fluctuating pattern. It is likely that our mid-term monitoring was not enough to find an explicit response to such environmental change, which could take several decades to emerge (Egerstone *et al.* 2004). Therefore, the short-term surveys of macrophytes studies which are increasing in the region (Padial *et al.* 2008) might not be able to assess the effects of global change.

SAV fluctuations in choked coastal lagoons are frequently observed (Flores-Verdugo *et al.* 1988; Medeiros-Dos Santos & Esteves 2004). During low salinity phases (< 10), SAV growth could be limited by resource availability, e.g. nutrients. If nutrients are not limiting, C and C-B species may increase biomass and cover. However, lower effects are expected in less favorable and predictable zones due to the lack of high biomass species. Therefore, the increasing coastal eutrophication could have important effects in choked lagoons, promoting higher fluctuations of SAV, where low vegetated phases may alternate with high vegetated ones during low and high salinity periods, respectively. Changes in salinity and trophic state took place several times during the Holocene in Laguna de Rocha (García-Rodríguez *et al.* 2004, Inda *et al.* 2006), indicating that SAV species have probably faced these long-term events recurrently.

Nutrient enrichment can promote the succession of primary producers, where Charophyte are first replaced by canopy forming angiosperms (Scheffer 1998), then angiosperms are replaced by Non-Charophyte macroalgae and finally phytoplankton can dominate (McGlathery 2001; Rabalais 2002). In Laguna de Rocha an *Enteromorpha* sp. proliferation was recorded in spring 2007, while a phytoplankton bloom was observed in seaward zones (Conde *et al.* unpublished data). Therefore, with cultural eutrophication primary producers could become increasingly variable, with alternating proliferations of macrophytes and other photosynthetic organisms.

Choked coastal lagoons, like Laguna de Rocha and other lagoons of the SW Atlantic, usually undergo artificial openings (Suzuki *et al.* 1998; Medeiros-Dos Santos & Esteves 2004; Chagas & Suzuki 2005). Changes in the fish assemblage were reported after artificial openings in Brazilian coastal lagoons (Saad *et al.* 2002). Our results suggest that the management of the sand bars of these lagoons can have important effects on the SAV community, mediated by changes in salinity. Since the salinity regime depends not only on the sand bar opening but also on freshwater discharge, evaporation, wind direction, as well as the geomorphology of the sand bar, hydrological studies and modeling are needed to explain the effects of sand bar manipulation on biological communities. Moreover, this information should be considered in decision models for artificial openings, especially if lagoons, like Laguna de Rocha, are included in conservation areas.

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**CAPÍTULO III: Modern vegetation and pollen analogs in four
Southwestern Atlantic coastal lagoons**

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ABSTRACT

Modern analogs and their relationship with actual vegetation facilitate paleoecological reconstructions while changes in pollen abundance are indicators of environmental fluctuations. We used recent pollen deposits in the sediments of Uruguayan coastal lagoons to obtain the modern analog of the vegetation in the catchment areas and analyzed the ephemeral but recurrent proliferations of submerged aquatic vegetation. We mapped the flora of four coastal lagoons, conducted samplings of submerged aquatic vegetation, and analyzed the pollen record in each lagoon. The sediment samples represented the last 60-90 years of deposition, and the flora of the catchment area was well represented in the pollen records. Submerged aquatic vegetation was present in all lagoons but ephemeral proliferations were not detected from the sediments. Conversely, a submerged vegetated phase was recorded in one lagoon while in other lagoons gaps in the pollen profiles were observed. Simultaneous botanical and pollen analyses better capture the large fluctuations of submerged aquatic vegetation in coastal lagoons.

Key words: modern analog, submerged aquatic vegetation, pollen, coastal lagoons.

INTRODUCTION

Coastal lagoons are among the most productive ecosystems in the world (Knoppers 1994), sustaining important ecosystem services such as fisheries (Pauly & Yáñez-Arancibia 1994) and are usually biodiversity rich ecosystems (Esteves *et al.* 2008). Uruguay's coastal lagoons are also rich in biodiversity and highly productive ecosystems (Bonilla *et al.* 2006; Aldabe 2010). These lagoons originated after marine transgressions and regressions during the Holocene (MTO *et al.* 1980), and are characterized by their intermittent connection to the Atlantic Ocean through a breach which opens naturally on their sand bars. Such natural dynamics drive steep salinity gradients which determine the ecological functioning of the whole ecosystem (Jorcín 1999; Conde *et al.* 1999; Bonilla *et al.* 2005; Piccini *et al.* 2006; Alonso *et al.* 2008). Paleolimnological studies have been conducted to determine the origin of the lagoons, the salinity and trophic state conditions during sea level fluctuations and the aquatic communities that dominated each phase (García-Rodríguez *et al.* 2004a; b; Inda *et al.* 2006a). Also, archeological studies have been conducted to determine the human relationships with these ecosystems (Inda *et al.* 2006b and references therein). However, paleobotanical studies of the terrestrial and aquatic vegetation of the lagoons are only recently being conducted (García-Rodríguez *et al.* 2010). The vegetation in these lagoons is characterized by diverse flora immersed in a matrix of natural prairies, where different types of sand dune communities, forests, shrublands and freshwater and saline wetlands are commonly found. Furthermore, in the water basin of the lagoons SAV is comprised of a diverse and fluctuating community of freshwater, brackish and marine tolerant species (Bonilla *et al.* 2006; Rodríguez-Gallego *et al.* 2010). Recent research revealed the important ecosystem roles of the SAV community in these lagoons. SAV not only acts as habitat for benthos (Arocena 2007) and food for aquatic birds (Sarroca 2008), it also intervenes in biogeochemical cycles trapping nutrients and suspended material during high biomass phases (Rodríguez-Gallego *et al.* 2010) and may act as a refuge for commercially important fish and crustaceans.

Ruppia maritima L. and other SAV species are abundant and well distributed at least in Laguna de Rocha and are frequently found in Uruguay's other coastal lagoons (Bonilla *et al.* 2006). Although limnological studies in Laguna de Rocha have been conducted since 1987, the presence of the abundant *R. maritima* was not recorded until 2001 (Rodríguez-Gallego *et al.* 2002) which was the first record of the species in the country. Similarly, abundant patches of *R. maritima* were found in Laguna Mar Chiquita in Argentina by Bortolus (2001) despite there was no botanical record of the species. In both cases, the absence of previous records could be due to incomplete botanical survey or to recent colonization by this cosmopolitan species. However, pollen analysis conducted in Mar Chiquita did not record *R. maritima* either (Stutz & Prieto 2003; Stutz *et al.* 2006), which supports the second assumption.

SAV ephemeral proliferations were observed in Laguna de Rocha, where biomass and covered area increased considerably during a few summer seasons. This phenomenon was explained by salinity and hydrological conditions. Nevertheless, anthropogenic eutrophication (Aubriot *et al.* 2005) and an increase in precipitation and runoff (Bates *et al.* 2008; Genta *et al.* 1998) could be promoting more frequent SAV proliferations (Rodríguez-Gallego *et al.* 2010). Similar processes could be occurring in other coastal lagoons, where local proliferation and sudden disappearance of SAV were observed, e.g. in Laguna de Castillos and Laguna Garzón (Rodríguez-Gallego unpublished data). The reason for the high variability of the SAV community in Uruguay's coastal lagoons is still unknown, driving researchers to ask new questions. Have the SAV species recently arrived in Uruguay's coastal lagoons? Are SAV proliferations periodical? Or are they responses to recent eutrophication and precipitation changes?

Pollen records obtained from lake sediment strata provide information on past vegetation composition (Faegri & Iversen 1989, Birks & Birks 1980, Prentice 1988). The study of modern analogs based on palynological assemblages and their relationship with actual vegetation allows for reliable paleoecological reconstructions (Behling *et al.* 2001; Mao *et al.* 2006; Masciadri 2009), which permits pollen indicators from different environments or plant communities to be identified (Stutz & Prieto 2003; Fontana 2005). Also, pollen grains from several taxa can be used to assign relative dates to sediment strata, for example when the date of introduction of exotic species is known (Birks & Godron 1985; Janssen & Birks 1994). Furthermore, changes in pollen abundance have been interpreted as a result of expansions or retractions of certain environments and their associated vegetation (Behling *et al.* 2001; Fontana 2005; Stutz *et al.* 2006). The study of pollen records in coastal lagoons may also be a powerful tool for reconstructing the terrestrial and aquatic flora and analyzing the dynamics of submerged aquatic vegetation (SAV thereafter). The aims of this article are to: 1) determine the relationship of plant communities in the catchment area of Uruguay's four choked coastal lagoons with the modern pollen assemblages in the upper 18 cm of sediments, 2) determine the presence of SAV species pollen in the sediments from the last number of decades and 3) analyze if SAV proliferations are recurrent events.

STUDY AREA

Uruguay is located in South America and is influenced by a subtropical to temperate climate with a mean rainfall of 1226 mm y^{-1} (mean annual precipitation in Rocha Meteorological Station from 1970 to 2006). Uruguay's coastal lagoon system is composed of four choked lagoons: José Ignacio, Garzón, Rocha and Castillos located in the Atlantic coast (Fig. 1, Table 1). These lagoons harbor important biodiversity values, and form part of the MAB - Biosphere Reserve Bañados del Este, and a Ramsar site. They are currently being inducted into Uruguay's National System of Protected Areas. The dominant land use in the catchment areas is cattle ranching on natural prairies. However, during the 1990's, land uses began to change and an expansion of afforestation with exotic trees (*Pinus* spp. and *Eucalyptus* spp.) and agriculture was observed (Rodríguez-Gallego 2010). Therefore, one of the main environmental concerns in these lagoons is eutrophication. Phosphorus appears to be increasing in Laguna de Rocha (Aubriot *et al.* 2005), possibly due to runoff from agricultural lands, although inputs from urban and rural population cannot be discarded. Episodes of potentially toxic cyanobacteria have already been observed in Laguna de Castillos (Pérez *et al.* 1999, Bonilla *et al.* unpublished data of 2010) and in Laguna de Rocha (V. Hein, unpublished).

Paleolimnological data are only available for Laguna de Rocha and Laguna de Castillos. Laguna de Rocha originated around 7000 yr BP and Laguna de Castillos 7000 - 7400 yr BP after the first large Holocene marine transgression. Afterwards, several sea level fluctuations drove the lagoons to alternate between marine or brackish/freshwater conditions (García-Rodríguez *et al.* 2004a; b; Inda *et al.* 2006a). Trophic state showed an inverse pattern with paleosalinity. Marine phases exhibited lower trophic states while a concomitant increase in trophic state was observed when salinity decreased (García-Rodríguez *et al.* 2004a; Inda *et al.* 2006a).

METHODS

Description of Vegetation

We obtained a map of the vegetation in the catchment area of Uruguay's four coastal lagoons (Fig. 1) after satellite image classification of a Landsat 5 TM (Path/Row 222-084, resolution of 25 m²) image from January 2005. We used automatically and supervised methods (Venturieri & dos Santos 1998) and also inspected Google Earth images and several series of aerial photographs to conduct some corrections. In the case of Laguna de Castillos we updated the vegetation classification using a CBR image from October 2009. Maps were validated in the field, taking ca. 1200 points (during 2006 and in Laguna de Castillos also during summer 2010). Classification errors were ca. 12%. The palm tree forests were digitalized from the topographic maps (1:50.000, Servicio Geográfico Militar of 1967) and coastal forests and shrublands were corrected after Bartesaghi *et al.* (2009a). SAV covered area was not estimated because it can not be determined in satellite images due the high water turbidity in the lagoons. The area of natural prairies was estimated after subtracting all vegetation types, urban, agriculture, afforestation and lagoon areas in the catchment areas. To determine the date of the *Pinus* spp. plantation in the coastal zone, aerial photographs of 1940 were inspected (Servicio Geográfico Militar).

The botanical description was based on published and unpublished data taken from Alonso-Paz & Basagoda (1999; 2006), Delfino *et al.* (2005), Delfino & Masciadri (2005), Fagúndez & Lezama (2005), Masciadri *et al.* (2006), Rodríguez-Gallego (2006), Brussa & Grela (2007), Bartesaghi *et al.* (2009a; b), Ríos (2009) and Rivas *et al.* (2010), as well as on qualitative field inspection and the authors' unpublished data. For SAV descriptions we conducted seasonal samplings during 2005 and 2006 to collect SAV biomass in the same sites where pollen corers were taken (see Fig. 1). SAV biomass was collected with an Ekman grab and then sorted by taxa. The plants' dry weight was estimated after 48 h at 80 °C. Charophytes could not be taxonomically discriminated. For Laguna de Rocha SAV biomass records are also available from 2001 to 2008 (Rodríguez-Gallego 2010) and for all lagoons qualitative SAV data is available from a sampling in summer 2004 (Rodríguez-Gallego unpubl.).

Pollen analysis

Pollen samples were taken manually with a corer (diameter: 6 cm) in the summer of 2006. We took one corer per lagoon, located on sites where SAV was frequently recorded and in semi-enclosed or open bays where hydrodynamics are low. In José Ignacio, plants were absent during the entire study but the sample was also taken in a semi enclosed bay. In Laguna de Castillos the corer was taken in the NW outlet of the Chafalote wetland, where hydrodynamics are low (Fig. 1). Sediment for pollen analysis was separated into strata every centimeter until a depth of 10 cm for Laguna de Rocha and Garzón. For Laguna de Castillos and José Ignacio sediment was separated into strata from 0 to 5 cm and from 6 to 10 cm to reduce the number of samples for analysis. Strata of deeper sediments (14 to 15 cm and ca. 16/17 to 17/18 cm) were also analyzed for every lagoon. Therefore, 12 samples per lagoon were analyzed for Laguna de Rocha and Garzón and four samples for Laguna de Castillos and José Ignacio. A volume of 0.1 cm³ of sediment was processed for pollen analysis, and standard palynological procedures were used with HCL, HF and acetolysis treatments (Faegri & Iversen 1989). Three Lycopodium commercial tablets were added to every sample before treatment to estimate total pollen concentration (Stockmarr 1972). A Nikon BX 40 microscope was used for pollen counting. Pollen samples were inducted into the Palinology reference collection of the Facultad de Ciencias - Universidad de la República (FPA 656 a 692).

Data analysis

A Principal Component Analysis (PCA) was conducted to analyze the distribution of the pollen counts of the most abundant species (> 1% of the total pollen of the sample) in the four lagoons and in the depth profile. In order to select between linear (PCA) and unimodal (Correspondence Analysis) response models, a preliminary Detrended Correspondence Analysis with log

transformed (log x+1) biological data was conducted. Since the length of the gradient was lower than 2, the PCA was preferred (ter Braak & Smilauer 1998).

RESULTS

Present vegetation in the coastal lagoons and their catchment areas

The vegetation in the catchment area of the coastal lagoons of Uruguay is highly diverse, showing different plant associations which conform a complex spatial pattern, mainly in Laguna de Castillos (Fig. 1). Natural prairies are the best represented vegetation type (Table 1), where the dominating families are Poaceae, Asteraceae and Leguminosae. Widely distributed along the grasslands are several types of native forests and shrublands. The most extensive forests and shrubland types are associated with rocky hills and valleys, named High-lands Forests and Shrublands (Table 1), whose characteristic species are *Scutia buxifolia* Reiss, *Blepharocalyx salicifolius* (Humb.; Bonpl. & Kunth) O. Berg, *Lithraea* spp., *Citharexylum montevidense* (Spreng.) Moldenke, *Schinus* spp., *Celtis* spp., *Myrsine* spp, *Zanthoxylum* spp. among others. Riparian forests are the second most extensive vegetation type (Table 1), distributed along the fluvial system, where more hydropohilic species are found such as *Pouteria* spp., *Phyllanthus sellowianus* Müll.Arg., *Cephalanthus glabratus* (Spreng.) K. Schum, *Sebastiania* spp., *Salix humboldtiana* Willd., *Erythrina crista-galli* L., *Allophylus edulis* (A. St.-Hil.) Radlk among others. Palm tree forests are characterized by grasslands with a high abundance of the palm tree *Butia capitata* (Becc.) Becc., which is present only on the North and eastern side of Laguna de Castillos. Hydrophil forests are very important on the NE side of Laguna de Castillos and dominated mainly by *E. crista-galli*, but also *Cephalanthus* spp. is frequently found. This forest type grows along older inactive shores of this lagoon and conform a sort of concentric forested bands interspersed to wet prairies in a spatially complex pattern. Laguna de Castillos and also Laguna Garzón are surrounded by a riparian forest that grows on their sediment banks. In Laguna José Ignacio and less frequently in Laguna de Rocha, small patches of this forest type are also found. The dominating taxa is *S. buxifolia* followed by *A. edulis*, *Myrsine laetevirens* (Mez.) Arechav. among others, while in Laguna de Castillos *Phytolacca dioica* L. is exceptionally abundant conforming the Ombú forest. Coastal forests and shrublands are located between the ocean and the lagoons, and the larger relicts are found in Laguna Garzón, followed by Laguna José Ignacio and, to a lesser extent, in Laguna de Rocha and Valizas Stream at the South of Laguna de Castillos. These forests and shrublands are dominated by *S. buxifolia*, *A. edulis*, *M. laetevirens*, *Daphnopsis racemosa* Griseb, *Colletia paradoxa* (Spreng.) Escal. and *Schinus engleri* F.A. Barkley, where *Ephedra tweediana* Fisch. & C.A. Mey. is frequently found.

On the seashore the mobile and stabilized sandy dunes are inhabited by psammophyl herbaceous vegetation such as *Panicum racemosum*, *Calycera crassifolia*, *Senecio crassiflorus*, *Calystegia soldanella* and *Ambrosia tenuifolia*, among others. Large and heterogeneous wetlands are also found surrounding these coastal lagoons. Laguna de Castillos and Laguna Garzón are dominated by freshwater taxa while Laguna de Rocha and Laguna José Ignacio and also Valizas Stream have mainly saltmarsh species. Flooded prairies are composed by species of Poaceae, Cyperaceae and Apiaceae, and *Eryngium pandanifolium* also is abundant. In the more frequently flooded sites of freshwater wetlands small emergent macrophytes are abundant (*Ludwigia* spp., *Althernathera philoxeroides*, *Sagittaria montevidensis*, *Echinodorus* spp., *Eichhornia azurea*, *Pontederia cordata*, etc.). Also, free-floating plants are found in freshwater wetlands (*Eichhornia crassipes*, *Pistia stratiotes*, *Salvinia* spp., *Limnobium laevigatum*, *Lemna* spp., *Richocarpus natans*, *Azolla* spp., among others) as well as water lilies (*Nimphoides indica* and *Hydrocleys nymphoides*). Closer to the edges of the lagoons in freshwater wetlands large emergent plants are abundant such as *Typha* spp., *Schoenoplectus giganteus*, *Schoenoplectus californicus*, *Zizaniopsis bonariensis* and *Thalia multiflora* while in saltmarshes *Spartina densiflora*, *Scirpus pungens* and *Juncus acutus* are more frequent and *Sarcocornia perennis* is also found.

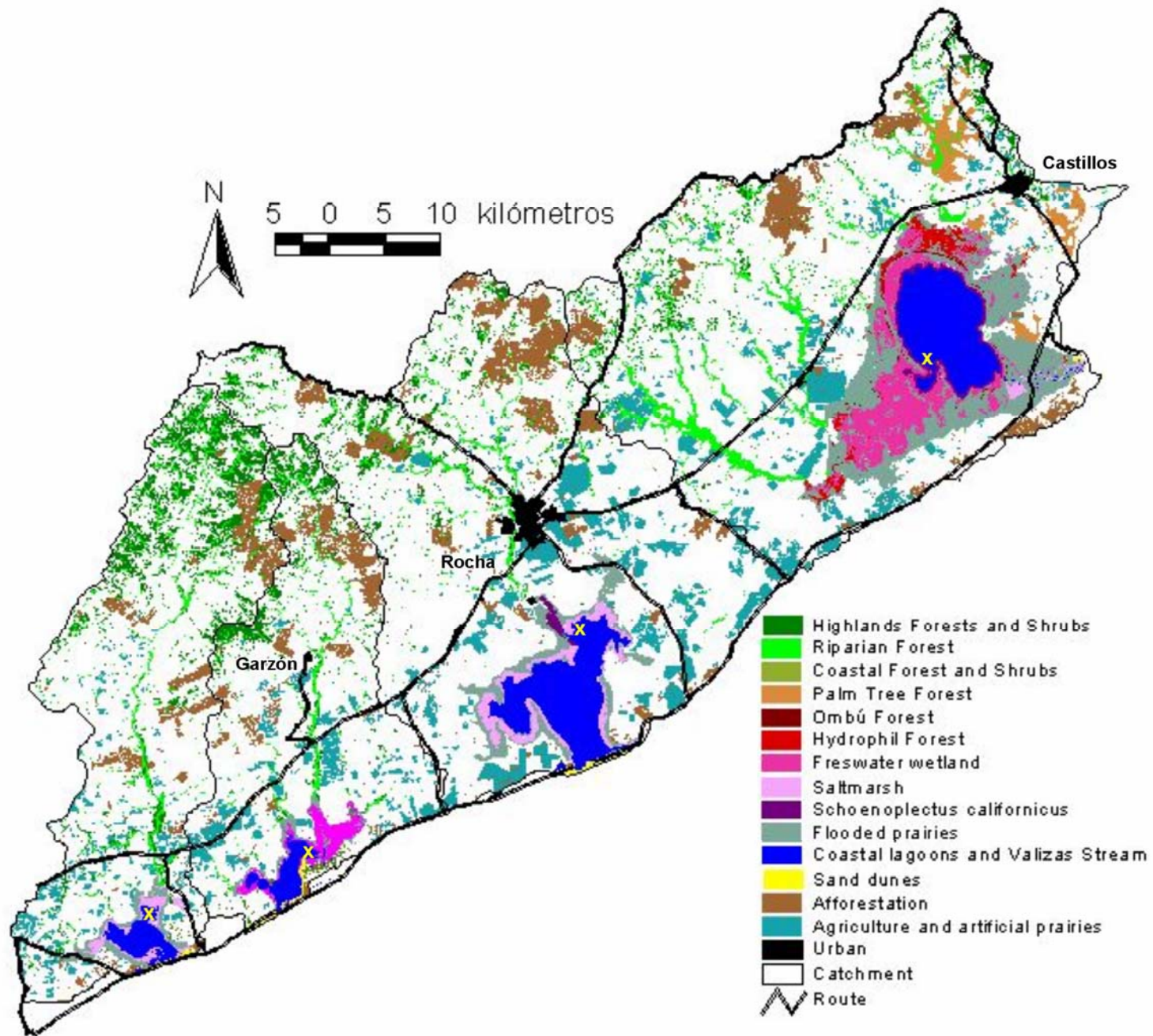


Fig. 1. Map of the catchment area of Uruguay's four coastal lagoons, indicating different vegetation types, main routes and towns. White crosses indicate the pollen sampling sites. The different vegetation types are located in a matrix of natural prairies which is not colored.

Table 1. Surface area of the different vegetation types in the catchment area of Uruguay's coastal lagoons. SAV-covered area was not estimated. The catchment and lagoons surface area were included.

	José Ignacio	Garzón	de Rocha	de Castillos	Total surface area (ha)
Natural prairie	47252	37378	80196	76505	241332
High-land forest and shrub	7809	3363	3565	2671	17408
Riparian forest	3507	2094	2741	6921	15262
Coastal forest and shrub	102	257	1	29	390
Palm tree forest	0	0	0	4073	4073
Ombú forest	0	0	0	255	255
Hydrophil forest	0	0	0	1549	1549
Freshwater wetland	0	1609	0	7279	8887
Saltmarshes	919	18	2603	321	3861
<i>S. californicus</i> wetland	0	0	303	1115	1418
Flooded prairie	1231	764	3771	13156	18922
Psammophilic herbaceous vegetation of sand dunes	126	269	273	47	715
Coastal lagoons and Valizas stream	1565	1503	7304	6921	17292
Catchment area	70358	56055	121433	136665	384511

SAV in the water body of the coastal lagoons is composed of brackish species (*Ruppia maritima*, *Zanichellia palustris* L., Charophytes, *Potamogeton pectinatus* L., *Eleocharis* sp. and *Myriophyllum quitense* HBK). However, submerged species non-tolerant to salinity are frequently found in the outlet of the streams and also in the freshwater wetlands (*Cabomba caroliniana*, *Egeria densa*, *Myriophyllum aquaticum*, *Potamogeton pusillus*, *Potamogeton ferrugineus* and also Charophytes). The SAV biomass registered in the pollen sampling sites during 2005 and 2006 is indicated in Table 2. Qualitative records of other SAV species during all samplings are also indicated. It is possible to observe that Laguna José Ignacio was un-vegetated during the entire study period and also during previous samplings (summer 2004, data not shown). On the other hand, Laguna de Rocha showed the highest richness of vegetation and SAV was present throughout the whole year. SAV communities in Laguna Garzón and Castillos fluctuated greatly, SAV was present only in autumn 2005 and summer 2006 and biomass and richness were generally lower.

Table 2. Mean (\pm standard deviation) biomass (g DW m⁻²) of SAV species in Uruguay's coastal lagoons. Biomass samples were taken seasonally from summer 2005 to autumn 2006 in the same sampling sites where pollen corers were collected. * indicates qualitative records of SAV species.

	<i>R. maritima</i>	<i>Z. palustris</i>	<i>P. pectinatus</i>	<i>M. quitense</i>	<i>Eleocharis</i> sp.	Charophytes
José Ignacio	0	0	0	0	0	0
Garzón	*	0.4 \pm 1.7	0	*	0	30.7 \pm 119
de Rocha	4.2 \pm 4.3	0.2 \pm 0.2	0.4 \pm 0.7	0.2 \pm 0.8	0.7 \pm 2.0	0.3 \pm 0.2
de Castillos	1.5 \pm 2.3	0.9 \pm 3.2	0	*	*	1.7 \pm 3.3

Pollen analysis

Twenty-nine pollen taxa were identified from a total of 3526 pollen grains counted from all lagoons, excluding spores (Fig. 2). Laguna Garzón and José Ignacio showed the highest pollen concentrations and richness and Laguna de Castillos the lowest. In addition, pollen richness decreased with depth while pollen concentration increased slightly. Pollen taxa from all lagoons was grouped into the following categories: terrestrial herbs, terrestrial trees and shrubs, freshwater emergent plants and SAV (Fig. 2). The terrestrial herbs included nine taxa

(Leguminosae were considered in this group) and were by far the most abundant group (63.9% of total pollen). Within this group, Poaceae accounted for 34.4% of the total pollen, followed by Chenopodiaceae (14.6%), Cyperaceae (10.3%) and Asteraceae (5.6%). Terrestrial trees and shrubs were the richest group, with 10 taxa including the exotic *Pinus* spp. This group had the second most abundant number of pollen grains (16.8% of the total pollen), with *Myrsine* sp. being dominant (5.2%), followed by *Celtis* sp. (3.9%) and Myrtaceae (1.6%). Freshwater emergent herbs were represented by seven taxa, making it quite rich in comparison with the other groups but with the lowest total pollen abundance (3.5% of the total pollen). Apiaceae was the dominant taxa in this group (2.3%). The SAV group was quite an abundant group in terms of total pollen (10.4%) but was composed of only three taxa, where *Myriophyllum* sp. was the most abundant (9.1% of total pollen), followed by *Potamogeton* sp. (0.8%) and *R. maritima* (0.5%).

A PCA conducted with all samples and lagoons and the most abundant taxa explained 62.7 % of the total variance, where the first axis separates lagoons (axis value of 0.29) and the second separates sampling strata (axis value of 0.16). The PCA identified four groups of samples: 1) superficial samples from Laguna Garzón and José Ignacio; 2) superficial samples from Laguna de Rocha, 3) deeper samples from Laguna Garzón and José Ignacio and 4) deeper samples from Laguna de Rocha and most samples from Laguna de Castillos, except the most superficial one which behaved completely different. The deeper and superficial samples from Laguna Garzón and José Ignacio were related between them, and groups 3 and 4 were more related also. Superficial samples tended to be all grouped together while deeper ones were also grouped. Cyperaceae, *Myriophyllum* sp. and *Ambrosia* sp. taxa were associated with deeper samples from Laguna Garzón and José Ignacio, while Poaceae, Apiaceae and several trees pollen grains were associated with surface samples from these lagoons and also from Laguna de Rocha. Chenopodiaceae and Asteraceae pollen types were more abundant in deeper samples from Laguna de Rocha and Laguna de Castillos, while SAV species such as *Potamogeton* sp. and *R. maritima* were more associated with surface samples from Laguna de Rocha. Spores were associated with deeper samples and mainly with Laguna de Castillos surface sample.

DISCUSSION

Modern pollen and present vegetation relationships

Modern pollen assemblages and vegetation of Uruguay's four coastal lagoons shows close similitude. The most abundant pollen group - terrestrial herbs - represents the dominant open landscape around all lagoons. Poaceae, Asteraceae and Leguminosae were among the most represented families in our pollen record and are also the most abundant in Uruguay's natural prairies (Marchesi 2004). Cyperaceae usually inhabits flooded prairies that surround the lagoons, with high abundances of *E. pandanifolium* while sand dune vegetation is represented mainly by pollen of *Baccaris* sp. and also Chenopodiaceae which is abundant in small wetlands in the sandy dunes. Moreover, lagoons surrounded by coastal forests and shrublands (Laguna Garzón and Laguna José Ignacio) showed higher richness and abundance of terrestrial trees and shrubs pollen types as *E. tweediana*, *Celtis* sp., *Daphnopsis* sp., and *Myrsine* sp. (Bartesaghi *et al.* 2009a,b; Ríos *et al.* 2009; Alonso-Paz & Basagoda 2006; Delfino *et al.* 2005). Pollen of these taxa was also abundant in Laguna de Rocha, although trees communities are quite distant from this lagoon. Coastal forests and shrublands are represented by tiny and dispersed patches along Laguna de Rocha margins (due to their small size they are not captured in the vegetation map), but pollen grains could also belong to the riparian forest and at least for *Celtis* sp. and *E. tweediana*, which are absent in the Rocha stream close to the lagoon (Masciadri unpublished), their origin may be the high-lands forests and shrublands. In the case of Laguna de Castillos, Anacardiaceae, *Myrsine* sp. and Mirtaceae pollen grains were observed. These taxa are abundant in the riparian forest that surrounds the lagoon (Rodríguez-Gallego 2006), while the low number of grains could be due to the poorer preservation conditions. Other wood types such as hydrophyll forest and the palm tree forest were not recorded. This again could be an effect of pollen preservation problems, but also taxonomic resolution could be improved, since the highest indeterminate number of pollen grains was found in this lagoon.

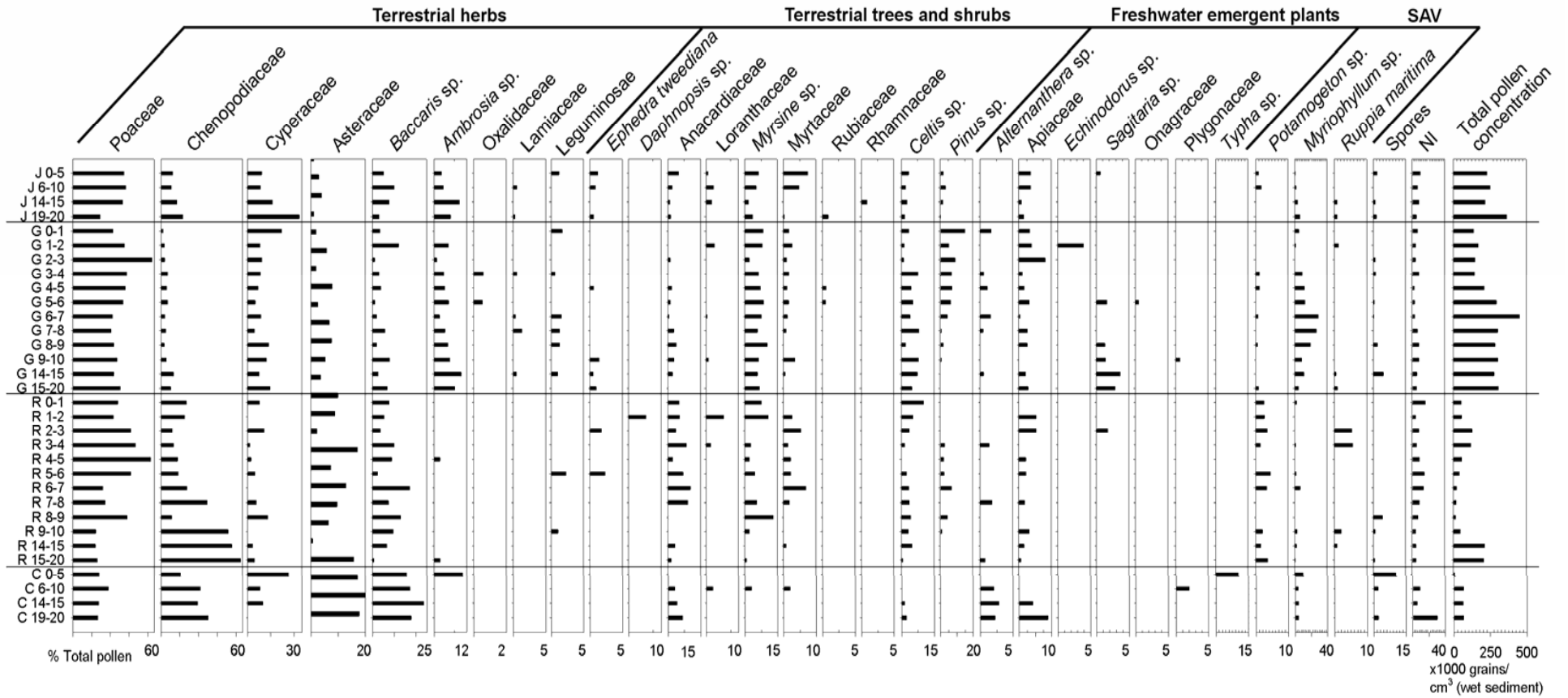


Fig. 2. Percentage pollen diagram of modern sediments from Uruguay's four coastal lagoons (José Ignacio-J, Garzón-G, Rocha-R and Castillos-C.). On the left, lagoons and depths strata are shown; lagoons are also separated by lines. On the right, total pollen concentration is presented. The different groups of pollen taxa are also indicated in the upper part of the diagram. NI: indeterminate pollen grains. Counts of the pollen taxa were expressed as a percentage of the total pollen including spores and indeterminate grains.

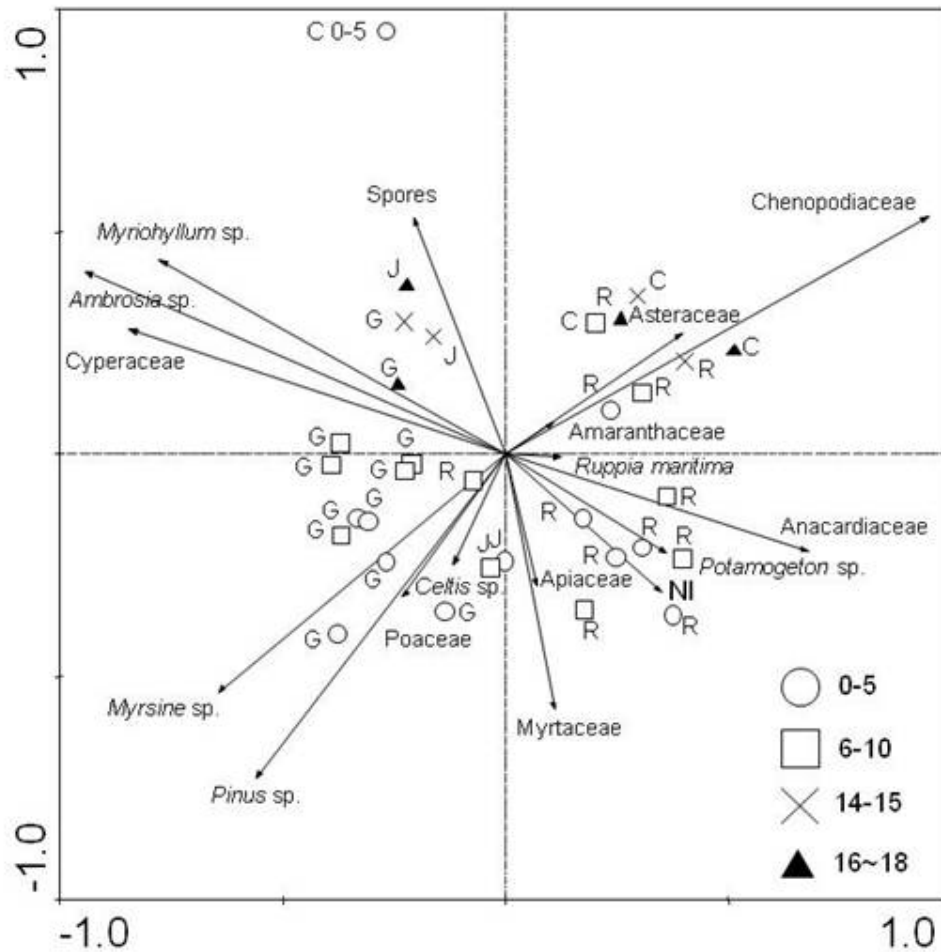


Fig 3. PCA biplot with the most abundant pollen taxa. Symbols indicate different strata; sample sites in each lagoon are also indicated (R- Rocha, C- Castillos, J- Jose Ignacio and G- Garzón).

Chenopodiaceae pollen was also related to coastal saltmarshes by Stutz & Prieto (2003) in Mar Chiquita coastal lagoon (Argentina). If Chenopodiaceae are indicators of saltmarshes, they might therefore be more abundant in the most saline systems, which seem to be the case in Uruguay's coastal lagoons. This taxa was poorly represented in Laguna de Garzón, where saltmarshes are almost absent, while it was abundant in Laguna de Rocha, José Ignacio and Castillos which show extensive *S. densiflora* saltmarshes. According to Isacch *et al.* (2006), Laguna José Ignacio has the most extended saltmarsh of Uruguay's coastal zone, while pollen of saltmarshes along the Valizas stream can be transported to Laguna de Castillos by SW winds and marine intrusions. The salinity range may explain these differences in vegetation. Laguna de Rocha and José Ignacio are the most saline (mean salinity: 13.7 ± 6.2 and 11.0 ± 5.6 , respectively during 2005-2006), whereas Laguna de Castillos and Garzón are the least saline (mean salinity: 3.9 ± 4.7 and 8.3 ± 5.4 , respectively). In the four lagoons Chenopodiaceae increased with sediment depth. This may be indicating that salinity in all lagoons could have been higher in past decades. This hypothesis is in agreement with precipitation increase in Uruguay since the 1970s (Bidegain *et al.* 2006; Genta *et al.* 1998), which is attributed partially to climatic change in the region (Bates *et al.* 2008). Therefore, consequences in wetlands dynamics can be expected, where saltmarshes may be decreasing in their extension. This may have implications for biodiversity conservation, decreasing the habitat for threatened species such as the Olrog's gull that feed in saltmarshes (*Larus atlanticus*, Yorio *et al.* 2005). Salinity fluctuations had been frequent during the evolution of these

lagoons, where several marine and brackish/freshwater phases were recorded in the fossil record of Laguna de Rocha (García-Rodríguez *et al.* 2004; Inda *et al.* 2006a).

The pollen from freshwater emergent plants showed the opposite pattern to Chenopodiaceae, exhibiting higher abundance and richness in the less saline lagoons. Laguna Garzón had the highest richness and abundance of freshwater emergent plants, since the pollen sampling point receives the outflow of an important freshwater wetland. In contrast, in Laguna de Rocha and José Ignacio pollen records from this group were almost absent. Apiaceae, however, was present in the four lagoons because *Hydrocotyle* spp., *Eryngium* spp. and *Lilaea* spp. taxa are frequent in the prairies with impeded drainage that surround the lagoons. Although Laguna de Castillos has the biggest freshwater wetland with a very rich species composition that drains towards the pollen sampling site, pollen from freshwater plants was not as abundant and rich as previously expected. In this lagoon Cyperaceae could be more related to the aquatic *S. californicus* and *S. giganteus* than to terrestrial herbs, since they are very abundant in the surrounding wetlands. Again preservation processes may be involved in Laguna de Castillo's impoverished pollen record.

SAV pollen was recorded in the four lagoons mainly due to the presence of *Myriophyllum* sp., while *R. maritima* and *Potamogeton* sp. were absent in Laguna de Castillos. Generally, pollen from less salinity-tolerant taxa was more abundant in the less saline lagoons. *Myriophyllum* sp. pollen was more abundant in Laguna Garzón, mainly in deeper zones but decreasing again after 8 cm. We considered this species to be *M. quitense*, a quite salinity-tolerant taxa (Orchard 1981) that was found inhabiting the water body of all coastal lagoons, except Laguna José Ignacio. In contrast, in more saline lagoons such as Laguna de Rocha and José Ignacio pollen of the seagrass *R. maritima* and *Potamogeton* sp. (possibly *P. pectinatus* which is frequently found in these lagoons) were more abundant, both being tolerant to brackish conditions (Kanthrud 1990, 1991). Nevertheless, in the streams and wetlands that surround the lagoons the strictly freshwater species *M. aquaticum*, *P. pusillus* and *P. ferrugineus* (Schütz Rodrigues & Irgang 2001) were also found (Rodríguez-Gallego, pers. observ.). However, fine pollen taxonomic discrimination is not possible with pollen grains from these taxa.

Generally, small lagoons better reflect local flora while larger lagoons capture the flora of larger areas (Suigita 2007; Masciadri 2009). Our pollen record reflected better the local aquatic flora but also the more distant terrestrial vegetation. Samplings for pollen analysis in the central zone of the lagoons could have had opposite results. Despite the low number of samples per lagoon and the different quantity of sediment strata analyzed in each lagoon the similitude between the pollen record and the present flora was high. Preservation problems in Laguna de Castillos may explain the absence of records from some communities as the palm tree and hydrophil forests. The different pollen concentrations among lagoons may also be reflecting different pollen preservation conditions. In Laguna Garzón and José Ignacio, where the pollen samples were taken from semi-enclosed bays, the pollen concentrations were higher, while in the other two lagoons samples were taken from open bays and the pollen concentration were lower. Nevertheless, to improve the modern pollen analog of Uruguay's coastal lagoons surface samples in other zones of the lagoons should be taken.

Sediment dating

Pollen records by themselves can be useful in obtaining relative sediment dates (Birks & Godron 1985, Janssen & Birks 1994). The exotic pines plantation in the coastal sand dunes can be used to date modern sediments in Uruguay's coastal zone. Pines plantations began marginally in 1920 in the Town of La Paloma near Laguna de Rocha (Gutiérrez-Laplace 2000) but it spread after 1940 (after inspection of aerial photographs from 1940). To the south of Laguna Garzón, the pines plantation began in 1947 (local inhabitant communication) and possibly in similar dates in Laguna José Ignacio, while in Laguna de Castillos it started in 1978 (Alonzo & Basagoda 2006). *Eucalyptus* spp. pollen grains were not discriminated from other native Myrtaceae, therefore interpretation of pollen data of this taxa should be carried out with caution and relative dating was not possible.

Pollen grains from pines were found in Laguna de Rocha until 10 cm strata, while in Laguna Garzón and José Ignacio until 14-15 cm, indicating relative dates of less than 86 and 59 years for these strata, respectively. Moreover, a change in pollen abundance and composition was evident from 8-9 cm strata for Laguna Garzón and Rocha and from 6-10 cm in Laguna José Ignacio. Deeper samples were clustered together and separated from superficial ones in the PCA. The deposition rate estimated by the pines pollen records from this study were 1.2 and 2.5 mm y⁻¹ for Laguna de Rocha and Garzón respectively. These rates are in agreement with the values reported by Inda *et al.* (2006a). We found pollen of SAV along the sediment profile in all lagoons, therefore these species were present in Uruguay's coastal lagoons since at least 59 to 86 years.

In contrast, pines pollen was not recorded in Laguna de Castillos. This could be due to the longer distance from the afforested sand dunes, but mainly due to the bad conditions for pollen preservation. Laguna de Castillos shows a different pollen profile, where the upper strata (0 to 5 cm) had the lowest number of taxa and a very low pollen concentration, while the following strata (6 to 10 cm) was clustered with the deeper samples of all lagoons. Also, the pollen grains from this lagoon were broken, smashed and cracked which are clear signs of transport and disturbances. These facts make it more difficult to interpret the pollen profile of this lagoon, but possibly the pollen samples might be older than expected. This coincides with results from García-Rodríguez *et al.* (2004b) of a paleolimnological survey in this lagoon, where modern sediments were not found. It is evident from our results that in fluctuating environments such as coastal lagoons future research should simultaneously conduct ²¹⁰Pb and ¹³⁷Cs dating and palynological analysis.

SAV dynamics

SAV in choked coastal lagoons is usually a highly dynamic community (Flores-Verdugo *et al.* 1988; Medeiros-Dos Santos & Esteves 2004; Rodríguez-Gallego *et al.* 2010) which seems to be also the case in Uruguay's coastal lagoons. During our SAV samplings, Laguna de Castillos and Garzón were vegetated only during autumn 2005 and summer 2006 and Laguna de Rocha was always vegetated. On the contrary, Laguna José Ignacio was not vegetated; despite the pollen record indicates that plants were present. Santana & Fabiano (2003) reported *Z. palustris* in Laguna José Ignacio, which is usually found together with *R. maritima* (Rodríguez-Gallego *et al.* 2010). In contrast, in Laguna de Castillos and Valizas stream (Rodríguez-Gallego, per. observ.) *R. maritima* biomass was observed with flowers and fruits, but it was not found in the pollen record. The pollen record seems to detect taxa with low abundances, that can disappear for long periods or that prefers to reproduce vegetatively such as *R. maritima* (Kantrud 1991) and *P. pectinatus* (Kantrud 1990) as in Laguna de Rocha. These species may have short flowering periods when conditions are favorable, and the pollen record may be able to capture this information while seasonal biomass surveys cannot. Therefore, a combination of botanical surveys and modern pollen records constitutes a powerful tool for determining the species composition of fluctuating SAV communities.

The SAV community in Laguna de Rocha showed itself to be highly dynamic. Species changes their abundance and cover from year to year and salinity seems to be the main factor explaining this pattern. Rodríguez-Gallego *et al.* (2010) described a SAV ephemeral proliferation in summer 2003, where most species increased their biomass. We did not detect SAV proliferations in the pollen record of this lagoon, *Potamogeton* sp. and *Myriophyllum* sp. were frequently found along the depth profile and *R. maritima* had only slight variations. Besides, the increase of *Myriophyllum* sp. in middle strata of Laguna Garzón may indicate that this species could have been more abundant developing a SAV phase, possibly during long periods of isolation of the lagoon from the ocean and therefore of low salinity.

The pollen record of the SAV species was highly variable in the coastal lagoons of Uruguay, which may indeed depict natural variability patterns in these communities. SAV might be in a state of permanent recolonization after local extinctions due to unfavorable conditions such as salinity

increases or water level fluctuations. This extinction-recolonization dynamic of SAV may scale up the trophic web. Benthos in Laguna de Rocha increases its abundance and richness in vegetated zones (Arocena 2007; Rodríguez-Gallego *et al.* 2010), which is one of the main energy pathway to higher trophic levels (Rodríguez-Graña *et al.* 2008). Moreover, the most important populations of the herbivorous black-necked swans are found in Laguna de Rocha and also Castillos that feeds on SAV (Sarroca 2008). Refuge and feeding areas for commercially important fish and crustaceans are presumed, since similar biomass values such as those found in Laguna de Rocha played similar roles in Mexican coastal lagoons (Pérez-Castañeda & Defeo 2004). Furthermore, SAV in Laguna de Rocha can intervene in biogeochemical cycles during high abundance periods, acting as a trap for suspended solids and total nutrients (Rodríguez-Gallego *et al.* 2010). Understanding the natural variability of such a relevant ecological feature in different time scales may help further understanding of the ecosystem functioning of highly dynamic choked coastal lagoons.

In summary, we found that: 1) recent pollen assemblages reflected the local flora well and to a lesser extent more distant vegetation types. 2) SAV species are present in Uruguay's four choked coastal lagoons and have inhabited these systems at least during the last c.a. 90 years. 3) The pollen record for SAV species showed several gaps in the depth profile, possibly indicating species absence, while abundant pollen records could indicate SAV dominance phases. The pollen record demonstrated to be a powerful tool for detecting species presence as a complement to snapshot botanical surveys, mainly for highly fluctuating communities such as SAV in choked coastal lagoons.

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**Capítulo IV: Land suitability assessment in the catchment
area of four Southwestern Atlantic coastal
lagoons: multicriteria optimization modeling**

Lorena Rodríguez-Gallego

ABSTRACT

In the present study, a Land Suitability Assessment (LSA) was conducted in the basin of four Uruguayan coastal lagoons (Southwestern Atlantic) to promote productive development while minimizing eutrophication, biodiversity loss and conflicts among different land uses. Suitable land for Afforestation, Agriculture, Livestock ranching, Tourism and Conservation sectors were initially established based on a multi-attribute model developed using a Geographic Information System. Specialists were consulted to determine the requirements for each land use sector and the incompatibilities among land use types. The current and potential conflicts among incompatible land use sectors were analyzed by overlapping land suitability maps. We subsequently applied a multi-objective model where land (pixels) with similar suitability was clustered into "land suitability groups", using a two-phase cluster analysis and the Akaike Information Criterion (AIC). Finally, a linear programming optimization procedure was applied to allocate land use sectors into land suitable groups, maximizing average suitability and minimizing interference among sectors. Results indicated that current land use overlapped by 4.7% with suitable land of other incompatible sectors. However, the suitable land of incompatible sectors overlapped in 20.3% of the study area, indicating a high potential for the occurrence of future conflict. The highest competition was between Agriculture and Conservation, followed by Afforestation and Agriculture, which were also the sectors most affecting the extension of other uses. We explored scenarios where Livestock ranching and Tourism intensified, and found that interference with Conservation and Agriculture notably increased. This methodology allowed us to analyze current and potential land use conflicts and to contribute to the strategic planning of the study area.

Key words: multicriteria modeling; multiobjective modeling; strategic planning; coastal lagoons; Uruguay

INTRODUCTION

Land suitability is defined as the fitness of a particular area for a specific use relative to the needs and potential of social factors (Bojórquez-Tapia *et al.*, 1994). Land Suitability Assessment (LSA) is a tool for territorial design which considers the physical and biological requirements for each sector activity, as well as the stakeholder interests and values (Malczewski *et al.*, 1997). Therefore LSA is highly dependent on the participatory process and representation of all land use interests (Bojórquez-Tapia *et al.*, 2004). Land use sectors are stakeholder groups that have similar uses or interests in a certain land surface, independent of whether they are landowners. Conflicts among land use sectors occur when sector activities jeopardize or reduce the capacity of other sectors to exploit a specific area, i.e. when competing land uses overlap in space (Bojórquez-Tapia and Ongay-Delhumeau, 1992). The primary advantage of LSA is its capacity to design sector uses that consider the land use suitability of small parcels (pixels). Pixels with similar suitability scores for different land sectors are grouped together, creating land suitability groups. A linear programming optimization procedure is subsequently conducted to allocate land use to the most suitable areas. When competing land use types overlap, the most suitable type is selected. Therefore, land suitability is maximized and conflicts minimized (Bojórquez-Tapia *et al.*, 2001). The assessment generates a map where all land sectors are allocated, derived from a systematic methodology and consultations with land use sector representatives. This methodology is increasingly used in environmental, urban and agricultural planning (Malczewski, 2006), and is especially suitable for strategic regional planning (Malczewski, 1997). Allocation of lands for forestry (Malczewski *et al.*, 1997), aquaculture (Bojórquez-Tapia *et al.*, 2001), agriculture (Boonyanuphap *et al.*, 2004), camping sites (Chow and Sadler, 2010), highways (Bojórquez-Tapia *et al.*, 2002) and even redefining boundaries of protected areas (Bojórquez-Tapia *et al.*, 2003, 2004) are all examples of how this methodology is currently applied.

Environmental legislation in Uruguay has evolved rapidly during the last 20 years. Beginning in 1997, environmental protection was explicitly declared of public interest in the Constitution. Contemporary legislation includes the Environmental Impact Assessment Law, the Environmental Protection Law and the National System of Natural Protected Areas Law, all of which provide opportunity for public consultation as well as land use assessment and planning. The recently approved Territorial Planning and Sustainable Development Law incorporates the concept of strategic planning. Due to the implementation of environmental legislation, stakeholders' participation has been legally guaranteed, promoting an emerging culture of

community involvement. Nevertheless, the application of modern environmental legislation in Uruguay is still ineffective. This is partially due to the absence of a transparent and robust territorial planning process, with appropriate analytical procedures that permit the integration of different disciplines, a broad knowledge base, and public participation.

Coastal lagoons are among the most productive ecosystems in the world (Knoppers, 1994), sustaining important ecosystem services (e.g. fisheries, Pauly and Yáñez-Arancibia, 1994) and are usually highly biodiverse (Esteves *et al.*, 2008). Nevertheless, these ecosystems are increasingly threatened by eutrophication, pollution, and urbanization due to the human population growth in coastal zones (Berkes and Seixas, 2005). In the southern region of South America, coastal lagoons are a common feature of the coastal zone. The four coastal lagoons of Uruguay sustain important fisheries (Fabiano *et al.*, 1998). Moreover, they are among the most diverse ecosystems in the country (Brazeiro *et al.*, 2008) and therefore more effective conservation efforts are demanded by several organizations and governmental agencies. Land use changes driven by agriculture, afforestation (the conversion of grasslands and shrublands to tree plantations, *sensu* Farley *et al.*, 2005) and tourism are ongoing and intensifying. Consequently, tensions between land users and conservationists are occurring, which are expected to increase if development continues to intensify without proper management.

LSA provides the opportunity for an interdisciplinary and participatory planning process with the aim of solving land use conflicts in at risk ecosystems, satisfying social demands and supporting environmental legislation. The goal of this study was to apply LSA for the first time in Uruguay to promote productive and tourism activities in the basin of four protected Atlantic coastal lagoons while minimizing eutrophication, biodiversity loss and land use conflicts.

MATERIALS AND METHODS

Study area

Four coastal lagoons are located on the Atlantic coast of Uruguay (Fig. 1, Table 1), which periodically connect with the ocean through a breach opened in their sand bars. This natural dynamic results in steep salinity gradients which determine the ecological functioning of the entire ecosystem (Bonilla *et al.*, 2005; Conde *et al.*, 2002; Piccini *et al.*, 2006; Rodríguez-Gallego *et al.*, 2010). The primary ecosystems in the lagoons catchment area include grasslands (savannas *sensu* Olson *et al.*, 2001), mixed with patches of natural forest; coastal sand dunes; and large areas of fresh and saline wetlands. These lagoons sustain approximately 52% of the bird species of Uruguay (Aldabe *et al.*, 2009; Rudolf, 1996) and several endemic species of vertebrates, invertebrates and plants, as well as relict and endangered forests (e.g. palm tree forests, and coastal forests and shrublands). Furthermore, these lagoons and their catchment areas provide important ecosystem services. The lagoons are nursery and feeding areas for coastal fish (e.g. white croaker, kingfish and flatfish) and crustacean (blue crab and pink shrimp) resources (Fabiano *et al.*, 1998), which sustain the coastal inland fisheries of Uruguay (Fabiano and Santana, 2006). The riparian vegetation of the fluvial system prevents eutrophication by buffering the runoff from agriculture and urban lands, which are rich in agrochemicals, nitrogen and phosphorus. These lagoons are part of a Biosphere Reserve (MaB-Bañados del Este) and the first Ramsar site (Wetland of International Importance) in Uruguay, and are being inducted into the National System of Protected Areas (SNAP). Recent studies identify these lagoons among the highest priority for biodiversity conservation in the country (Brazeiro *et al.*, 2008). Furthermore, their outstanding landscapes sustain a growing tourism industry.

The human population is relatively low (36903 inhab.; 91.6% urban), with less than one person per 10 ha (Table 1). The most important land use sectors include Livestock ranching, Agriculture, Afforestation, Tourism, Fisheries and Conservation (Rodríguez-Gallego *et al.*, 2009). Extensive livestock ranching on natural grasslands is the dominant economic and therefore land use activity (71% of the entire surface area, MGAP-DIEA 2000). However, in the 1990s shifts in agricultural practices were reported. Potato, soybean, and forage cultivation and the introduction of artificial prairies increased 3% from 1997 to 2005, and afforestation with exotic species (eucalyptus and pines) increased 5%. In the coastal zone, traditional "sun and beach" style tourism expanded from villages (where populations exhibited a 10-fold increase during summer) into natural zones. However, new tourism modalities are emerging in the study area, due to a growing preference for natural or rural areas with attractive landscapes.

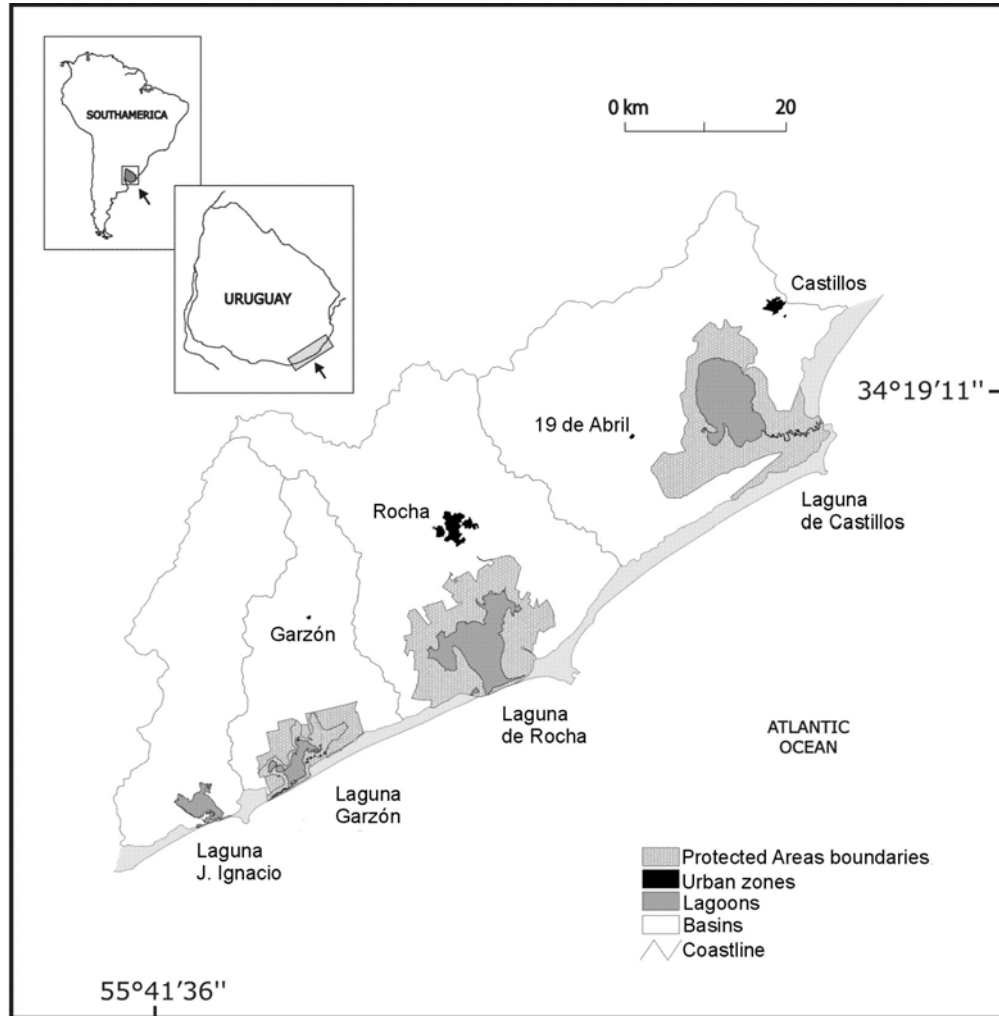


Fig. 1. Map of the study area indicating the delimitation of the actual and the proposed protected areas. The coastal strip outside the lagoons' basins (grey area) was excluded from the study.

Major environmental concerns in these lagoons include nutrient increases (Aubriot *et al.*, 2005) due to runoff from agricultural lands and sewage discharge, overfishing (Fabiano and Santana, 2006), hydrological alterations and anthropization, all driving biodiversity and productivity loss as well as landscape homogenization. Therefore, increased tensions between conservation and traditional development have been expressed. Currently, the most pressing conflict is between conservation and urbanization for traditional tourism development. However, disagreement among productive sectors has also emerged (e.g. ranchers organizing themselves against afforestation expansion) and a general concern about soybean agriculture is ongoing. These disagreements will increase if land use intensification continues without a global planning intervention.

Table 1. Physical and socioeconomic description of the coastal lagoons of Uruguay and their basins.

	José Ignacio	Garzón	de Rocha	de Castillos
Area in ha. (lagoon and catchment) (km ²)	13 / 848	18 / 695	72 / 1312	90 / 925
Human settlements and other influencing tourism zones	J. Ignacio village, Santa Mónica and Eden Rock seaside resorts, influence of Punta del Este tourist area	Garzón village, influence of Punta del Este tourist area	City of Rocha, influence of the town of La Paloma	City of Castillos, 19 de Abril village, influence of the villages of Valizas, Cabo Polonio and Aguas Dulces
Inhabitants (2004 census)	894	606	26527	8874
Afforestation during 2005 (ha)	4360 (6%)	4221 (8%)	8578 (7%)	5983 (4%)
Agriculture and artificial prairies during 2005 (ha)	3488 (5%)	4561 (8%)	10922 (9%)	9432 (7%)
Extensive Livestock ranching during 2005 (ha)	46392 (66%)	40033 (71%)	83912 (69%)	104062 (76%)

Methodology

The LSA was conducted following Bojórquez-Tapia *et al.* (2001, 2004). The study area was comprised of the catchment area of the four coastal lagoons (382,205 ha). The coastal strips between the lagoons were excluded (see Fig. 1). These areas are not included in the lagoons' basins and show a different and complex arrangement of ecosystems, stakeholders and conflicts. The land use sectors analyzed were Afforestation, Agriculture, Tourism, Livestock ranching and Conservation. Each sector included different production modalities, but was characterized by the dominant modality. Fisheries sector was not considered in the model because the land affected by the fishing villages is smaller than our pixel size while the entire lagoons surface are used for fishing activities.

The methodology followed four steps:

1) Specialist consultation

We conducted interviews with specialists from each sector (an architect specialized in territorial planning, an agronomists for the agriculture sector and an other one for the livestock sector, a forestry technician and specialists in the conservation sector), all of which had experience in the study area. The specialists were asked to define: a) the sector objectives and activities; b) the environmental characteristics required for each land use type i.e. criteria and attributes (see Table 2); and c) the incompatibilities with other land uses. Incompatibilities occurred when two sectors competed for land, and therefore the activity of one sector decreased the yield of another sector (Bojórquez-Tapia *et al.*, 1994 and references therein). For the Conservation sector we consulted several ornithologists and one ichthyologist to develop distribution maps that characterized the main biodiversity values. We provided the conservation specialists a spatial distribution map of the main environments. They subsequently assigned a list of species of SNAP conservation priority to each environment, according to their own records and bibliographies. We performed the forest classification and the allocation of ecosystem services which were the filtering, retention and bank protection capacity of the riparian vegetation and wetlands, the corridor function of riparian and high-land forests and the coastal protection and sand bar maintenance conducted by the sand dunes. The ecosystem services were also assigned to each environment.

2) GIS database

Ecosystems and land use were determined on a Landsat TM 5 (Path/Row 222-084, resolution: 30 m) image from summer 2005, using a combination of automated and supervised techniques (Venturieri and dos Santos, 1998). The classification was field verified, where 1200 evenly distributed points were inspected. Classification errors were estimated in 12% of the check points, which is among acceptable values. Spatial attributes were represented in a vector format and transferred to a vector grid of 1 ha size, where each cell represented a pixel. Spatial Analysis and Image Analysis of ArcView 3.2 software (ESRI), Viewshed function of Spatial Analysis of ArcGIS 9.2 (ESRI) and Polygeom of Infremer were used to conduct all spatial analyses and GIS manipulations.

3) Multi-attribute modeling

A GIS-based sector suitability assessment was first performed independently for each type of land use. A thematic map represented each criterion and its attributes; pixels in the grid took on different values for each attribute. All attributes were standardized to a unique value scale for comparability. Value functions were utilized for continuous variables and a Hierarchical Analytical Process (AHP) for nominal variables (Pereira and Duckstein, 1993). These functions transferred the specific value of each land attribute to a utility score in a [0,1] interval scale. Criteria for each sector were weighted using AHP (Saaty, 1980) manually programmed in an Excel spreadsheet, which generates weights in a [0,1] interval scale. We conducted attribute standardization and weighting, with the exception of Conservation, where the SNAP Biodiversity Officer was consulted.

The sector suitability score (s) of a specific land use sector was calculated using a weighted linear combination of all attributes (x) and their criterion weights (w) for each pixel (k):

$$S^k = \sum_i^I w_i Uf(x_i^k) \quad (1)$$

where S^k is the sector suitability in pixel k , w_i is the relative importance or weight of each criterion and $Uf(x_i^k)$ was the value function of attribute i at pixel k . S^k values can fall between 0 and 1. Restrictions of equation (1) are described in Bojórquez-Tapia *et al.* (2001). The sector suitability score was derived separately for each land use sector. The suitability score for each land use sector was also represented on a grid map.

4) Multi-objective analysis

The five sectors' suitability maps were numerically classified to obtain homogenous land use parcels or "land suitability groups". This procedure aggregated pixels according to their similarities in suitability scores for the different land types. We used a Two Phase Cluster (SPSS 11.5 software) analysis to classify pixels instead of the Polythetic Divisive Method used by Bojórquez-Tapia *et al.* (2001, 2004). The clustering method determines an optimum number of clusters, comparing each of the cluster solutions using the Akaike Information Criterion (AIC). AIC reflects the model parsimony combining goodness-of-fit and the number of estimated model parameters (Akaike, 1973). Outlier selection was performed with noise handling at 25%. The pixel classification was then exported to ArcView to create the land suitability group nominal map, where homogeneous suitability land parcels were depicted. Originally, cluster analysis identified six land suitability groups; however biodiversity specialists disagreed with one of the sectors (which grouped Tourism, Conservation and Livestock ranching together) and proposed dividing it into two new groups, one containing the Conservation suitable pixels and the other comprised of the remainder of the pixels, which were manually separated.

From the nominal map, an average land suitability matrix was calculated. Simple matrix algebra in ArcView was applied to average suitability scores by sectors (columns, j) and land suitability groups (rows, g). The averaged matrix was then double-centered by rows and columns to obtain Gower residuals, following Bojórquez-Tapia *et al.* (1994, 2001). We plotted the land suitability groups and sectors in a multiple bar chart against Gower residuals. Positive Gower residual values indicated high suitability for a specific land use in each land suitability group. Positive Gower residuals for antagonistic land uses represented conflicts among land use types.

Land suitability (suitability of all land use sectors cumulatively) was maximized and conflicts among sectors minimized by conducting a 0-1 mathematical programming procedure (Ragsdale, 2004) with Solver in an Excel spreadsheet. The objective function was as follows:

$$\text{Maximize } \sum_j z_{gj} y_{gj} \quad (2)$$

where the sum of the average land suitability for all land use sectors (z_{gj}) was maximized. The average land suitability was taken as the decision variables matrix (y_{gj}). After optimization, the decision variables (y_{gj}) took values of 0 if land use j in land group g was not selected, or 1 otherwise. The optimization procedure was subject to several restrictions:

$$Z_{gj} \in Z \quad (3)$$

$$Y_{gj} + y_{gh} \leq 1 \quad \forall j \neq h \quad (4)$$

$$Y_{gj} = 0, 1 \quad (5)$$

Restriction (3) assured that all sectors were considered, (4) avoided the selection of antagonistic land use and (5) indicated that the decision variables could only take values of 0 when the activity could not be conducted, or 1 when it could be conducted in a specific land suitability group.

RESULTS

Criteria and attribute description, valuation and weighting

The criteria and attributes identified by the specialists, value functions and weights are shown in Table 2. The Afforestation sector selected a single criterion "priority soils for afforestation" (as indicated in the Uruguayan legislation by the Decree n° 191 of 2006), however specialists indicated no distinctions among soil types. The Livestock ranching specialist also selected a single criterion "soil aptitude", where soil types exhibit different utility values (based on CONEAT Units, which classifies soils according to Livestock ranching productivity (MGAP, 1976)). The Agriculture specialist identified two criteria, the most important was "soil aptitude" (based on CONEAT Units) followed by "slope"; utility increased with soil aptitude and decreased with

slope. The Tourism specialist selected, in decreasing order of importance: 1) "distance to the ocean", 2) "view to the lagoon", 3) "flooding frequency" and 4) "conservation category". The first two were binary criteria, and had increased utility due to their landscape values. Low flooding frequency had intermediate utility because it represented safer housing conditions, while the conservation category (zones adjacent to protected areas) was preferred because management plans assured a certain degree of "wilderness" with acceptable restrictions to activities.

The Conservation specialists identified six criteria (Table 2), where weighting was based on importance to ecosystem function, eutrophication prevention and biodiversity values. Brackish ocean-connected lagoons (including the Valizas stream) had higher utility values than lagoons isolated from the sea. These ecosystems define the region and exhibit higher biodiversity and ecosystem services. Sand bars determine the natural functioning of the coastal lagoons and also have important conservation values, e.g. increased presence of endemic species. Wetlands with emergent macrophytes provide habitat for several bird species and act as a natural filter for runoff from the basin. Littoral vegetation areas associated with low order streams were assigned the high utility values because they serve to filter water from large zones of the catchment, while maximum order streams were also assigned greater utility value as they naturally filter the city sewage waters. The utility of the natural forests was set according to their uniqueness, representativeness and vulnerability, while coastal prairies were chosen due to the several migratory endangered species that inhabit the prairie ecosystem (e.g. buff-breasted sandpiper, *Tryngites subruficollis*).

Sector suitability

Specialists concluded that Afforestation competes with Agriculture, Tourism and Conservation due to the effects on soils and landscapes. Agriculture (in its current and more intensive modality) was considered incompatible with Conservation due to the replacement of natural habitat, agro-chemicals applications and contribution to eutrophication. Livestock ranching and Tourism in their current modalities were considered compatible with Conservation, since both are developed without severe modifications to the natural ecosystems. Sector suitability was segregated in space, but with significant overlap (Fig. 2). Agriculture competed with Conservation in 43.7% (47234 ha) of its suitable land, mainly in areas with riparian vegetation and in highland forests, but also in wetlands suitable for rice cultivation. Afforestation interfered with 37.8% (42690 ha) of the land suitable for Agriculture, but primarily in highlands, where suitability for agricultural practices is lower. Furthermore, Afforestation interfered with Conservation in 22.7% (24580 ha) of its suitable land, mainly in highland forests and areas with riparian vegetation. In contrast, Afforestation exhibited low interference with Tourism (7.8%, 8896 ha). Furthermore, lands with potential conflict represented 20.3% of the entire coastal lagoons' catchment area. Livestock ranching, the most compatible land use, overlapped with suitable terrestrial lands of all other sectors, followed by Tourism which overlapped with 40% (43638 ha) and 47% (115237 ha) of suitable Conservation and Agriculture lands, respectively, coinciding with their high suitability scores.

Presently, Livestock ranching is the only sector using most of its suitable area (77%), while Afforestation and Agriculture have low occupation rates (21 and 12%, respectively). Tourism maintains a very low proportion of its suitable lands, although no accurate data regarding its current distribution is available for comparison. Afforestation has the highest current interference with other sectors, affecting 3.7% of Agriculture, 2.7% of Tourism and 1.8% of Conservation suitable lands. The suitable areas for Conservation and Afforestation are a respective 1.6 and 1.2% affected by Agriculture. Therefore, Afforestation and Agriculture exhibit the highest interference between the two sectors and Agriculture and Conservation are the most affected. Finally, protected areas (Fig. 1) include 62.7% of the Conservation suitable lands with higher suitability scores, leaving ecosystem services such as eutrophication prevention outside the boundaries. This result can be explained by the fact that most of the natural forests are located in the highlands.

In addition, sector activities were observed outside the areas identified as suitable. Afforestation occupies 7690 ha (33% of the current afforested lands) apart from its priority soils. At least 3700 ha were identified in the recently established afforestation sector, located close or adjacent to Afforestation priority soils. The remainder of the afforested surface is composed of

small patches designated for cattle protection and old afforestation planted to stabilize sand dunes in the coastal zones several decades ago. Meanwhile, Agriculture only maintains 5% of its current area planted outside suitable agricultural lands.

Table 2. Criteria and attributes that determine land use sectors suitability. Weights and utility values are shown.

Sector/Criteria	Attribute	Weight	Utility
Forestry			
	Priority soils for afforestation	1	1
Livestock ranching			
Soil aptitude	Very low	1	0.04
	Low	1	0.10
	Medium	1	0.27
	Medium to High	1	0.59
Agriculture			
Soil aptitude	Very low	0.86	0.06
	Low	0.86	0.19
	Medium	0.86	0.74
Slope	0, 1, 2, 3	0.14	1
	4	0.14	0.67
	5	0.14	0.33
Tourism			
	Lagoon view	0.33	1
	Distance to the sea (less than 1 km)	0.51	1
Flooding frequency	Below the 5 m topographic curve	0.12	0.08
	Between the 5 and 10 m topographic curves	0.12	0.23
	Above the 10 m topographic curve	0.12	0.70
Conservation category	Zone adjacent to a Protected Area	0.04	0.73
	Proposed to become a Protected Area	0.04	0.20
	Protected Area	0.04	0.07
Conservation			
Type of lagoon	Periodically connected with the ocean and Valizas stream	0.34	0.86
	Isolated from the ocean	0.34	0.14
	Sand bars	0.28	1
Wetlands with emergent macrophytes	Natural vegetation belt along the fluvial system	0.16	1
	Order of the streams 2, 3, 6	0.11	1
	Order of the streams 4	0.11	0.50
	Order of the streams 5	0.11	0.25
Natural forests	Palm tree forest	0.07	0.16
	Ombúes forest (<i>Phytolacca dioica</i>)	0.07	0.27
	Psammophyl bush of low density	0.07	0.04
	Psammophyl forests of high and mid density	0.07	0.46
	Psammophyl forests of low density	0.07	0.05
	Fluvial and high-lands forests	0.07	0.03
Coastal prairies		0.04	1

Until now, Livestock ranching and Tourism were considered activities compatible with other land practices. Nevertheless, we explored scenarios where Livestock ranching intensified and replaced natural grasslands with artificial prairies, consuming high quantities of fertilizers; and situations where Tourism evolved into densely urbanized modalities. Under these conditions,

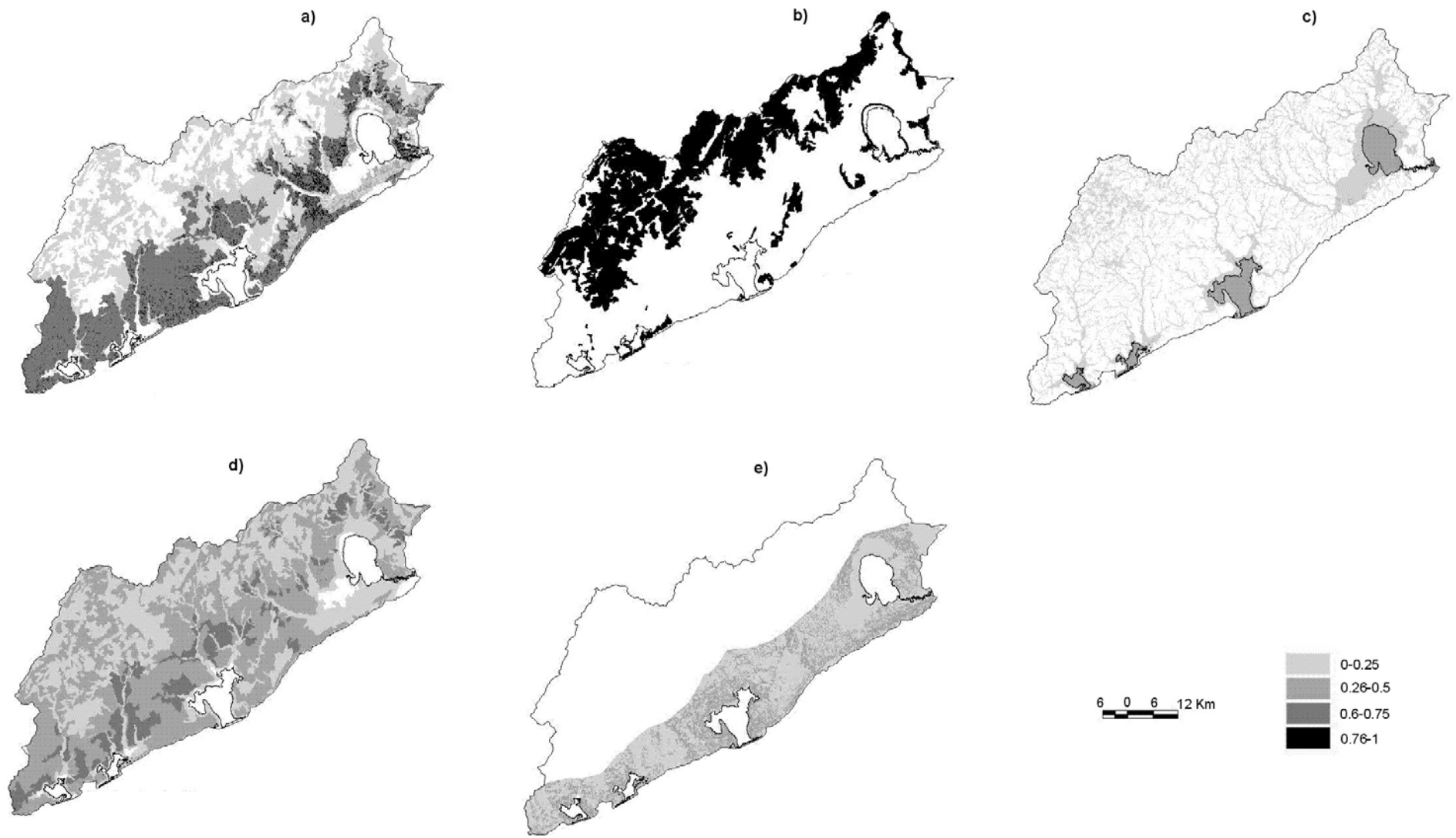


Fig. 2. Sectors' suitability maps of Agriculture (a), Forestry (b), Conservation (c), Livestock ranching (d) and Tourism (e). The grey scale represents the suitability scores from 0 to 1, ordered in quartiles.

new incompatibilities and potential conflicts with Conservation and Agriculture have the potential to occur. Results suggested that an increase in Tourism density could compete with up to 40% of the suitable Conservation lands and with 47% of the areas amenable to Agriculture (of mid to high suitability scores). Conflicts between intensified Livestock ranching and Conservation could be even greater, affecting 75.7% of the Conservation suitable area.

Multi-objective optimization

Following a numerical classification of the sectors' suitability maps, we obtained seven land suitability groups (Fig. 3A). The most suitable sectors were assigned to each group following inspection of Gower residuals (hereafter indicated with the capital letter of all suitable sectors) (Fig. 3B). Two land suitability groups were more appropriate for Agriculture (A) and Livestock (L) ranching (AL and LA), with higher scores for Agriculture in AL. Afforestation (F) characterized one group (F) and Tourism (T) and Agriculture were clustered (TA). Conservation (C) was represented in three land suitability groups, including Conservation and Tourism (CT); Conservation, Livestock ranching and Tourism (CLT); and Tourism, Conservation and Afforestation (TCF), with the highest scores found in CT. The highest average suitability score was detected in the F group (Fig. 3B) while the lowest average suitability scores were observed in the CLT and TCF groups (Table 3), indicating that suitability is low for most land uses.

The optimization procedure did not select Afforestation from the CTF group or Tourism from the F group, which represents a restriction of 2.8 and 2.2% of their respective suitable lands. Similarly, Agriculture was not selected from the CT, CTF and F groups, which represents 1.8, 2.6 and 17.3% of the respective Agriculture suitable lands. Agriculture suitable lands in the F and CT groups showed low suitability scores, however scores were notably high in the CTF group but the surface area affected was low (Fig 3, Table 3). Conservation was not selected from AL, LA, CLT and F groups by the optimization procedure, which represents, respectively, 6.6, 26.2, 19.8 and 3.9% of the Conservation suitable lands. The removal of Conservation from these land suitability groups suggested that 56.5% of the Conservation suitable areas could be lost; however, average suitability in these groups was low (Table 3), representing mainly riparian vegetation zones and forests. Alternatively, Livestock was selected in all land suitability groups by the optimization procedure.

Table 3. Average suitability and average surface values in hectares (between brackets) of each land use sector in the seven land suitability groups. Acronyms are defined in the text.

Land suitability group	F	L	A	T	C
AL	0.000 (0)	0.270 (60409)	0.652 (60410)	0.044 (33024)	0.010 (7112)
CLT	0.000 (0)	0.177 (95792)	0.064 (64918)	0.015 (25693)	0.015 (28323)
CT	0.000 (0)	0.016 (6981)	0.023 (4338)	0.007 (12944)	0.241 (31668)
CTF	0.204 (3141)	0.103 (14319)	0.135 (6340)	0.252 (15027)	0.122 (15397)
F	1.000 (107194)	0.167 (107193)	0.021 (42293)	0.002 (3250)	0.011 (21439)
LA	0.000 (0)	0.590 (31835)	0.646 (31835)	0.050 (16457)	0.011 (4270)
TA	0.066 (2559)	0.299 (38137)	0.465 (35019)	0.412 (38847)	0.000 (0)

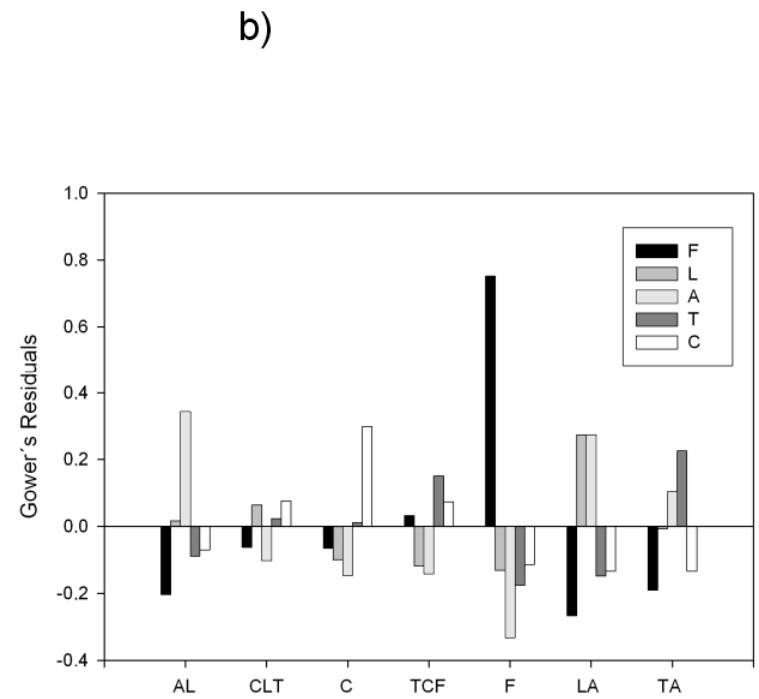
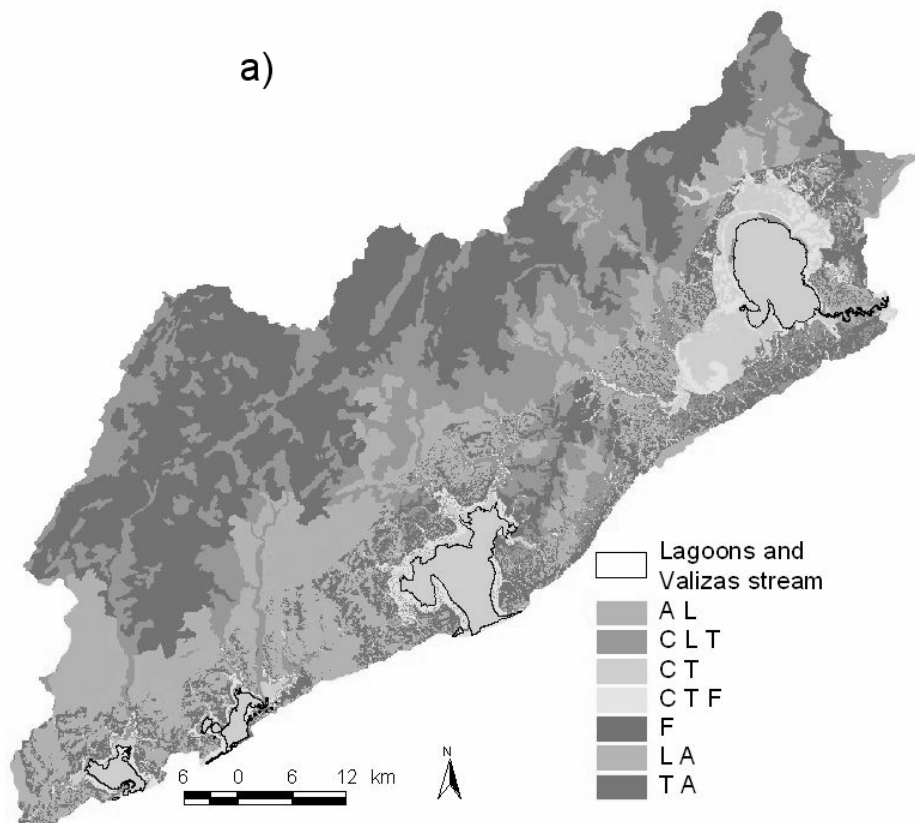


Fig. 3. a: Land suitability map showing the seven land suitability groups. The box indicates the allocation of sectors to each group according to their mean suitability. b: Bar chart of the Gower's Residuals plotted against the suitability groups; land use sectors are indicated. Acronyms are indicated in the text.

When Tourism was considered incompatible with Conservation, the optimization procedure removed Tourism from CT and Conservation from CTF, which affected 8.9% of Tourism and 14.2% of the Conservation suitable lands. When Livestock ranching was considered incompatible with Conservation, the procedure removed cattle ranching from CT and Conservation from CTF, which influenced Livestock ranching suitable regions in 2% and Conservation in 14.2% of their suitable areas. Finally, when Tourism was considered incompatible with Agriculture, an optimal solution was not found.

DISCUSSION

During the last 20 years, conflicts have frequently emerged between the conservation and economic sectors in coastal lagoon basins of Uruguay, primarily due to increasing environmental awareness on the part of stakeholders. We determined that in some cases competition among interests exist, but conflicts do not develop. In addition, our results indicated that perception of conflicts that initially appeared important exhibited less competition than expected when further analyzed. We found an overall 4.7% interference among current land use in the study area; however, this small value is sufficient to promote conflict among sectors and national and municipal authorities. Disagreements over urban development plans for coastal zones, division of wetlands, afforestation in highlands and soybean agriculture are increasingly common in the region, and in some cases has promoted disputes with the government (e.g. private urbanization in the Laguna Garzón protected area and illegal channels in Laguna de Castillos). We found that the most extensive current competition was between Afforestation and Agriculture, which are also the sectors that most affect other land use practices. Conservation was the second most affected sector, after Agriculture, but the surface area influenced was 3.8% of its suitable area. Furthermore, the analysis of sector suitability generated surprising results; the sectors with highest incompatibilities with other uses (Afforestation and Agriculture) made low use of its suitable land. Therefore, a major question resulting from our study is what will happen if these sectors continue to expand? Our analysis suggests that environmental conflicts will undoubtedly intensify and that emergence of new conflicts among land use will also increase.

The analysis of suitable lands for all sectors showed a marked increase in potential conflicts, and interference changed from 4.7 to 20.3% of the study area. In surface terms, Conservation would be the most affected land use type. Afforestation would replace it in 22.7% and Agriculture in 43.7% of its suitable area. However, Agriculture is also highly affected by Afforestation, where 42690 ha could develop conflicts. In both cases, interference would occur in the lower score suitable lands. Furthermore, our analysis underestimated Conservation conflicts, because natural prairies were not considered as a conservation criterion due to the lack of accurate and thorough information for the study area. Interferences may increase if extensive Livestock ranching and urbanization for Tourism intensifies, where Conservation and Agriculture may become the most affected uses. Nevertheless, currently protected areas in the entire study region appear effectively designed. Approximately 63% of the suitable Conservation lands are within the limits of the protected areas and are situated on lands with the highest suitability scores. However, we only analyzed the protected areas boundaries, and did not evaluate their Management Effectiveness (*sensu* Hockings *et al.*, 2006). For example, the two largest protected areas in this region maintain only one park ranger each (other two rangers have just been hired for Laguna de Rocha) and most park boundaries are still under review. The circumstances surrounding the Biosphere Reserve and the Ramsar Site are even worse due to the absence of management plans and personnel. This unfortunate circumstance of "paper parks" explains why the Conservation sector is increasingly active.

Other interference among sectors should be considered if land use suitability is to be maximized. For example, the expansion of sectors outside their suitable area should be avoided, primarily to guarantee acceptable sector performance but also minimize natural resource degradation. Therefore, special attention should be placed on Afforestation because 33% of this activity is located outside the afforestation priority soils, while the other sectors seem to conform to their suitable lands. Furthermore, the Conservation sector in Uruguay is also concerned with the impacts of Afforestation on water yield. Farley *et al.* (2005) revision demonstrated reductions in annual runoff from afforested lands that caused and intensified water shortages. In Uruguay Silveira and Alonso (2009) found similar results, however the proportion of basins that could be afforested without affecting water balance has not been addressed. Unfortunately, this was not analyzed in our study due to the coarse resolution of the

land suitability groups. Finer resolution procedures within each homogeneous group, where pixels themselves are optimized and Afforestation is allocated without exceeding certain surface thresholds, possibly near 10-20% of each tributary basin should be required.

Based on these results, the need for a participatory land use planning process in the coastal lagoon basins of Uruguay is evident, not only for preventing conflicts, but also for promoting the expansion of some sectors into their underused suitable lands. For example, the Tourism sector represents 26.8% of the Laguna de Rocha basin total economic value (a rough estimate), Afforestation and Agriculture 7.3 and 4%, respectively, and the protected area option value was 11% (Rodríguez-Gallego *et al.*, 2009). Given the economic relevance of these activities, both at the local and national levels, further expansion into their suitable areas should probably be promoted.

The approach used in this study provides a meaningful means to identify, understand, structure and solve conflicts in areas with alternative and competing uses overlapping in space (Malczewski *et al.*, 1997). Once conflicts are determined, the cause-effect relationships can be diagnosed and appropriate management guidelines generated (Bojórquez-Tapia *et al.*, 1994). Pixels clustering with AIC was a simple, one-step methodology to determine the optimum number of land suitability groups. However, statistical clustering should not be considered rigidly, and if specialists and stakeholders feel more comfortable with modifications to the clusters, further subdivisions should be permitted. However, caution is recommended and supporting arguments are required.

Land use ordering obtained by a multi-objective procedure would undoubtedly avoid conflicts. However, this approach suggests that all sectors, with the exception of Livestock ranching, commit some lands with the aim of preventing opposition and land suitability maximization, which is undoubtedly a complex task. It must be noted that the optimized suitability map represents an ideal scenario that is only intended for planning purposes, and following it strictly is neither possible nor recommended, since many land uses have already been developed. However, this map is a foundation for negotiation and can aid governments in designing new incentives for the development of sectors, simultaneously taking into account potential conflicts among groups and potential suitability loss. Therefore, this methodology can become a powerful analytical tool, allowing simulation of alternative scenarios and hypothesis testing (Ligmann-Zielinska *et al.*, 2008).

A closer inspection of potential new conflicts should be conducted, especially considering the compatibilities and incompatibilities among sectors. For example, Livestock ranching was considered compatible with Afforestation, but Afforestation may decrease cattle raising performance, land ownership changes and the displacement of local populations. Therefore, social and economic aspects other than suitability should be modeled, widening the goals of the planning process i.e. by including total economic value (including option and indirect values), number of jobs (Chuvienco, 1993) or human wellbeing attributes. Bojórquez-Tapia *et al.* (2001) reported that even if the recommendations of the planning process are not implemented by government agencies if the participatory process is genuine and results of studies robust, stakeholders themselves are likely to incorporate recommendations into their own planning process.

This planning methodology serves to effectively apply environmental legislation and is especially useful for strategic planning on a regional scale (Malczewski *et al.*, 1997). Furthermore, when local decisions are needed to define spatial allocation of sectors in each land suitability group, other multi-objective methods can be applied, including annealing procedures (Santé-Riveira *et al.*, 2008), genetic algorithms (Stewart *et al.*, 2004) or other neighborhood analyses (Ligmann-Zielinska *et al.*, 2008). In addition, a genuine participatory process should be ensured for a successful strategic planning process, including specialist and all other relevant stakeholders.

In summary, in the catchment areas of the Uruguay coastal lagoons, competition occurs among different land uses, and the potential for conflict development exists if land use continues to intensify. Conservation suitable lands are among the most affected, but greater competition occurs between Agriculture and Afforestation. The need for strategic planning that includes stakeholders' opinions is clearly evident to minimize opposition and promote expansion of

intensive land uses. The GIS-based LSA is a robust methodology to allocate land use in the Uruguayan territories while minimizing conflicts, and can aid in satisfying social demands and support legislation.

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DISCUSIÓN GENERAL Y PESRSPECTIVAS

En las lagunas costeras de Uruguay se observan indicios claros de un proceso de eutrofización antrópica, en algunos casos es un proceso incipiente (lagunas costeras que mantienen aún la conexión con el mar) y en otros está completamente establecido (Laguna de Diario). Floraciones de cianobacterias fueron registradas al menos en Laguna de Rocha (Hein datos sin pub.) y de Castillos (Pérez *et al.* 1999, Bonilla 2010 com. pers.) a la vez que se observó un incremento de las concentraciones mínimas de fósforo en la Laguna de Rocha entre 1981 y 2003 (Aubriot *et al.* 2005). Diferentes indicadores de estado trófico muestran que esas lagunas son generalmente mesotróficas a eutróficas (Bonilla 1998, Conde *et al.* 1999). Por el contrario, en la Laguna del Diario las plantas sumergidas son muy abundantes y la carga interna de nutrientes es muy elevada (Kruk *et al.* 2009). Al analizar los posibles aportes de nutrientes a estos cuerpos de agua se observa que algunas lagunas tienen poblaciones humanas importantes y que los usos agropecuarios se han intensificado, a la vez que nuevos usos se han establecido como la forestación con especies exóticas (Rodríguez-Gallego *et al.* 2009).

Esta tesis aportó una serie de evidencias acerca de los efectos de los usos del suelo en los indicadores de eutrofización y contribuyó a la planificación de los usos en la cuenca para minimizar sus impactos. Para esto se abarcaron secuencialmente los siguientes aspectos: el aporte de nutrientes desde las cuencas a las lagunas, el efecto de los aportes de nutrientes y los usos del suelo en los indicadores de eutrofización, los efectos de la conexión entre las lagunas y el mar en los indicadores de eutrofización, los efectos de la eutrofización y la conexión con el mar en la abundancia de productores primarios y la planificación de los usos del suelo para minimizar sus impactos en la calidad del agua y la biodiversidad. Para esto, se combinaron investigaciones realizadas a diferentes escalas espaciales y temporales y que analizaron diferentes aspectos del funcionamiento natural de estos sistemas, tanto a nivel de cuenca como de los cuerpos de agua. Dicha estrategia de estudio contribuyó a determinar el funcionamiento general de estos ecosistemas y su respuesta a los impactos generados por los usos del suelo en la cuenca.

Aportes de nutrientes desde las cuencas a las lagunas costeras

En la cuenca de las lagunas costeras de Uruguay se constató una intensificación de los usos del suelo en las últimas tres décadas, lo que se vio reflejado en la carga de nutrientes que podría estar siendo exportada a los cuerpos de agua (Fig. 3, Cap. I). Estos resultados apoyan la primer predicción del estudio, que plantea que la carga de nutrientes exportada desde la cuenca hacia las lagunas habría aumentado desde 1974 al 2005. La ganadería extensiva se intensificó, y existe una creciente sustitución de praderas naturales por praderas artificiales y siembras en cobertura, las cuales requieren fertilización (Fig. 2, Cap. I). A la vez, se observó un aumento de la superficie de campo natural que es sustituido por alguna forma de agricultura, actividad que se acerca cada

vez más a las lagunas. Sin embargo, estos usos no alcanzan el 7% de las cuencas aún (sin considerar el espejo de agua) (Tabla 2, Cap. I). Por otra parte, la forestación con especies exóticas era marginal a comienzos de los 90 pero en 2005 alcanzó el 7% de la superficie de las cuencas (sin considerar el espejo de agua). Por su parte, la población humana se mantuvo más o menos similar, aunque se crearon nuevos balnearios muy cercanos a las lagunas, mientras que en el caso puntual de Laguna del Diario la población en la cuenca se disparó sensiblemente en el último período intercensal (INE 2004). Además en la temporada de verano la población visitante se ha incrementado notoriamente en todos los balnearios cercanos a las lagunas, aunque no contamos con esos datos.

El aumento de la carga de nutrientes en el tiempo fue más marcado en las dos lagunas con mayor población humana (Laguna del Diario y de Rocha). Sin embargo, a excepción de Laguna de Diario donde la carga se incrementó drásticamente, en las restantes lagunas costeras el aumento fue moderado (Fig. 3, Cap. I). Al desglosar la carga de nutrientes por fuente se observa que el campo natural bajo ganadería extensiva, debido a su mayor superficie, y la población humana, por sus elevados coeficientes de exportación, son las mayores fuentes de nutrientes, mientras que el mejoramiento de campo incrementó sus aportes hacia los últimos años. Esto indicaría que si bien la agricultura aporta nutrientes a los cuerpos de agua, en la cuenca de las lagunas costeras no se habrían alcanzado niveles significativos aún. Por el contrario, el aporte de la ganadería extensiva, pese a que no requiere insumos de fertilizantes, puede ser importante en términos absolutos, por la gran superficie ocupada. En tal sentido, se requiere aplicar diversas medidas de manejo para minimizar la exportación de nutrientes a los cuerpos de agua, tanto para mitigar los aportes de la población humana, de la ganadería extensiva como de la agricultura. Ante un proceso de eutrofización antrópica la primera medida es explorar las fuentes de nutrientes del sistema en estudio, de manera de evaluar las medidas de manejo requeridas (Ryding & Rast 1992). Los análisis de carga de nutrientes utilizando coeficientes de exportación son una forma rápida y sencilla de determinar los usos con mayor potencialidad para la exportación de nutrientes. Sin embargo, la carga estimada es una medida grosera que puede no alcanzar los cuerpos de agua si se manejan los procesos de transporte por escorrentía o lixiviación desde sistemas de tratamiento. El siguiente paso, una vez determinado el panorama general de los usos que más aportan nutrientes, es realizar un análisis de las zonas de mayor riesgo de exportación a escala de predios agropecuarios, para obtener una cuantificación más precisa (sensu Sharpley *et al.* 2003).

Los aportes por la población humana podrían tener efectos muy drásticos, al menos en las dos cuencas más pobladas y especialmente en Laguna del Diario por su pequeño tamaño. Sin

embargo, estudios ecológicos realizados en el Aº Rocha que recibe los efluentes de la planta de tratamiento de OSE en la Ciudad de Rocha mostraron una rápida recuperación de la calidad del agua, aguas abajo de la ciudad, debido posiblemente al efecto depurador del bosque y humedal ripario (Arocena *et al.* 2000, Conde *et al.* 2010). Esto indicaría que en el caso de la Laguna de Rocha el impacto del aporte de nutrientes desde la ciudad no sobrepasaría la capacidad de depuración del ecosistema. Sin embargo, estudios hidrológicos que permitieran cuantificar el balance de nutrientes entre diferentes compartimientos son relevantes para evaluar si los nutrientes recibidos están siendo acumulados en el sedimento (Søndergaard *et al.* 2004.), desarrollando una carga interna que pueda desencadenar problemas de calidad del agua en el mediano plazo. Este habría sido el caso de Laguna del Diario, donde la carga de nutrientes recibida desde la cuenca fue acumulada en el sedimento, lo que desencadenó una elevada producción de biomasa de plantas sumergidas, afectando severamente el funcionamiento natural del sistema. En todos los casos se requiere analizar en más detalle el sistema de saneamiento, ya que se desconoce el grado de conexión de las viviendas y su eficiencia en remover los nutrientes, a la vez de analizar los aportes por la población rural dispersa y de los balnearios y poblados adyacentes a las lagunas, los cuales pueden tener aportes muy elevados y directos a los cuerpos de agua (Jarvie *et al.* 2006).

Efecto de los aportes de nutrientes desde las cuencas en los indicadores de eutrofización

Se constató una clara disminución de los valores de los indicadores de eutrofización con la superficie de bosque nativo, una ausencia de relación con la forestación, ganadería extensiva y población humana y efectos moderados y variables de los otros usos del suelo (Fig. 5, Cap. I). La reducción de los aportes de nutrientes por el bosque ripario está ampliamente reconocida en la bibliografía, donde se destaca a este ambiente como un importante filtro y sumidero de los nutrientes aportados desde la cuenca. Esta comunidad es un complejo de árboles, arbustos e incluso herbáceas de alto y pequeño porte que filtran la escorrentía y retienen sólidos en suspensión a la vez que incorporan nutrientes (McKergow *et al.* 2003 y referencias en el). La ausencia de efectos de la forestación (Fig. 5, Cap. I) podría deberse a su mayor distancia a las lagunas, ya que esta actividad se desarrolla en la cuenca alta. Asimismo, el manejo realizado de estas plantaciones podría explicar también la ausencia de impactos, ya que aplican fertilizantes únicamente al comienzo de la plantación y presentan rotaciones de varios años, a la vez que la vegetación riparia generalmente es conservada. Sin embargo, no descartamos que la no detección de impactos de la forestación en la calidad del agua se deba a que es una actividad recientemente implantada en la zona de estudio. Los efectos de la carga de nutrientes exportada por la agricultura fueron menos marcados. Por ejemplo, el fósforo fue mayor en lagunas con

más agricultura, lo que podría deberse al significativo aumento en el aporte de sólidos en suspensión observado en cuencas más agrícolas, mientras que el nitrógeno disminuyó. Además, las cuencas que exportan mayor cantidad de nutrientes por ha presentan un significativo aumento del fósforo del sedimento. La ganadería no presentó efectos en los indicadores de calidad del agua, posiblemente debido a que es la actividad basal en la cuenca y a que presenta los menores coeficientes de exportación de nutrientes. La ausencia de relaciones entre la población humana en los indicadores de eutrofización no tuvo una explicación clara, sin embargo, sus efectos estarían contemplados en la carga de nutrientes exportada por hectárea. En general, los suelos más superficiales y de menor fertilidad coincidieron con menores concentraciones de nutrientes en las lagunas, mientras que los suelos de mayor aptitud para la agricultura tuvieron mayor aporte.

Estos resultados indicarían que: 1) los aportes desde la cuenca no son suficientemente elevados como para generar aumentos destacados de nutrientes en las lagunas y/o 2) que existen procesos intermedios que retienen o minimizan los aportes desde las cuencas. La carga de nutrientes exportada por unidad de superficie hacia las lagunas coincide con los valores en cuencas con usos mixtos, que a su vez son menores que en cuencas predominantemente agrícolas (May *et al.* 2001 y referencias citadas), indicando que la carga de nutrientes exportada hacia las lagunas costeras no es preocupantemente elevada. A su vez, la reducción del nitrógeno observada en las cuencas más agrícolas podría deberse al menos a dos procesos complementarios. Por un lado, la desnitrificación que puede ser muy destacada en ambientes costeros como las lagunas, la cual a su vez aumenta con los aportes de nutrientes (Nixon *et al.* 1996). Por otro lado, la co-limitación de nitrógeno y fósforo que suele caracterizar a los productores primarios acuáticos (Bonilla 2002) podría implicar que al aumentar el aporte del fósforo desde la cuenca aumentaría el consumo del nitrógeno favoreciendo su disminución. Esto apoyaría el supuesto de que existen mecanismos que interceptan los nutrientes, previo a su llegada a los cuerpos de agua o que favorecen su reducción, disminuyendo los impactos en su calidad.

En el caso de los humedales, si bien se reconoce que cumplen funciones de retención de nutrientes (Mitsch & Gosselink 2000), en este estudio encontramos un patrón inverso que el nitrógeno fue más elevados en las lagunas con mayor relación entre la superficie de humedal y la superficie de laguna (Fig. 5, Cap. I). Esto podría deberse a que sería el bosque ripario quien estaría cumpliendo con la función de filtro, dado que la mayor superficie de intercambio entre usos del suelo y los cuerpos de agua ocurre a través del sistema fluvial y no de las márgenes de las lagunas. A su vez, dado que los humedales se ubican fundamentalmente adyacentes a las

lagunas y ambos sistemas están altamente ligados hidrológicamente, es posible que los humedales estén aportando a las lagunas materia orgánica particulada y disuelta rica en nutrientes, actuando como transformadores y no como sumidero de nutrientes. Sin embargo, se requieren más estudios para comprender mejor el patrón observado.

Los resultados obtenidos permitieron confirmar parcialmente la predicción de que los usos del suelo aumentan los valores de los indicadores de eutrofización, ya que esto fue observado en parte para la agricultura y la exportación de nutrientes por ha, pero no para la forestación, ganadería e incluso población humana. Los resultados sugieren que para precisar la relación entre los usos del suelo en la cuenca y los indicadores de eutrofización de las lagunas costeras es necesario abrir nuevas líneas de investigación, concentrándose en procesos que ocurren a escala de sitio. La función del bosque ripario como filtro de las actividades agropecuarias debería ser cuantificada a escala local, posiblemente en bosques en diferente estado de conservación, para entender los mecanismos involucrados. Por otra parte, la función de fuente o sumidero de nutrientes de los humedales debería ser analizada en mayor detalle, donde los procesos de desnitrificación requerirían especial atención.

Efectos de la conexión de las lagunas con el mar en los indicadores de eutrofización

Al analizar la relación entre los indicadores de eutrofización en las lagunas costeras y la salinidad se observó una clara influencia de la misma (Fig. 5, Cap. I). En general los valores de los indicadores de calidad del agua disminuyeron con la salinidad. Por el contrario, la Laguna del Diario cuya conexión con el mar fue interrumpida y por tanto no tiene influencia salina, presentó los mayores niveles de los indicadores de eutrofización. Los resultados obtenidos permitieron verificar la predicción que postula que la conexión de las lagunas costeras con el mar disminuye la eutrofización, mientras que su interrupción favorece su aumento. El incipiente proceso de eutrofización en las lagunas costeras, exceptuando Laguna del Diario, puede ser debido a que los aportes de nutrientes no son aún muy elevados y/o a que existen mecanismos o procesos que están contrarrestando los aportes desde la cuenca. La exportación de sedimentos y masas de agua desde las lagunas al mar mediante la conexión intermitente y el efecto de dilución provocado por el ingreso de agua marina (Suzuki *et al.* 1998, Kjerfve 1994, Smakhtin 2004), son un mecanismo adicional y de gran magnitud que también estría contrarrestando el aporte desde la cuenca.

El caso de la Laguna del Diario es particularmente extremo pero igualmente informativo. El elevado aporte de nutrientes desde la cuenca habría disparado un intenso proceso de eutrofización, sin embargo, la alteración de la conexión con el Río de la Plata que erradicó el

intercambio de agua entre ambos sistemas habría contribuido sustancialmente con dicho proceso. El aporte de nutrientes sumado a la imposibilidad de exportar sedimentos y agua al mar habría provocado la acumulación de sedimentos, nutrientes e incluso biomasa de plantas dentro de la laguna, que habrían sido exportados al mar de haberse mantenido la dinámica natural. El aporte de nutrientes se debió al drástico incremento de la población humana en la cuenca de esta pequeña laguna, lo que habría potenciado sustancialmente el desarrollo de la carga interna de nutrientes. Si bien existe conexión al saneamiento, esta no es completa ni totalmente efectiva. A su vez, otros mecanismos están relacionados a la interrupción del intercambio de masas de agua dulce y marina, potenciando la hipereutrofización del sistema. Por ejemplo, el ingreso de agua salada disminuiría la biomasa vegetal ya que las especies tolerantes son de pequeño porte, a la vez que se alteran los complejos ciclos biogeoquímicos, redox-dependientes, que modifican el reciclaje de fósforo y el ciclo del nitrógeno, aumentando su disponibilidad (Cronwell *et al.* 1996). Pese a que los impactos en la dinámica natural de esta laguna fueron muy elevados, sus consecuencias están atenuadas debido a que el sistema se estabilizó en una fase de agua clara dominada por plantas acuáticas. Sin embargo, dicho estado podría cambiar a uno dominado por algas potencialmente tóxicas, ya sea por el incremento de nutrientes (Scheffer *et al.* 2001) o debido al manejo de las plantas sumergidas (van Nes *et al.* 2002), que se realiza para mitigar los impactos estéticos y recreacionales, pudiendo empeorar aún más su situación y aumentar los riesgos para la salud humana.

Si bien el efecto en la calidad del agua del cierre permanente de la conexión de una laguna costera es claro, especialmente si el aporte de nutrientes desde la cuenca es alto, no es tan evidente el efecto de las aperturas artificiales en las restantes lagunas costeras. Generalmente, las barras arenosas son abiertas artificialmente cuando las lagunas aumentan su nivel y no se conectan naturalmente. Dicho manejo se realiza para evitar inundaciones en urbanizaciones mal planificadas o para promover el ingreso de larvas de recursos pesqueros. Es posible que las aperturas artificiales realizadas por maquinaria pesada alteren además la dinámica geomorfológica del sistema dunar, con efectos desconocidos. Una apertura artificial realizada durante 2003 mantuvo a la Laguna de Rocha abierta por más de ocho meses, siendo la apertura más larga registrada (Rodríguez-Gallego *et al.* 2010). Se desconocen las consecuencias de esto en la dinámica de nutrientes y la sedimentología, así como en el régimen salino. Si bien a *priori* realizar aperturas artificiales frecuentes parecería beneficioso, ya que mantendría las condiciones para la exportación de nutrientes desde las lagunas al mar, aparentemente las conexiones artificiales no desarrollarían igual competencia para el transporte de sedimentos, debido a modificaciones morfológicas en el canal de conexión, favoreciendo la sedimentación.

Evidentemente, para establecer el impacto de las aperturas artificiales se requieren estudios geomorfológicos y modelación hidrodinámica, combinados con estudios ecológicos.

Efectos de la eutrofización y la salinidad en las comunidades de productores primarios

La salinidad influyó la abundancia de las tres comunidades de productores primarios, provocando una disminución en la abundancia del fitobentos y de las plantas sumergidas y un aumento del fitoplancton (Fig. 5, Cap. I). A excepción de las plantas sumergidas, el efecto de la salinidad habría estado relacionado a otras causas como la resuspensión, concentración de nutrientes en el agua y disponibilidad de luz. A su vez, las abundancias del fitobentos y del fitoplancton mostraron una tendencia inversa entre sí. En general, el fitobentos se comportó de manera similar al nitrógeno, disminuyendo su abundancia cuando el nitrógeno disminuyó. Las causas que explican este patrón no son claras, pero tal vez procesos de desnitrificación en las lagunas podrían desfavorecer a esta comunidad. El tamaño de la cuenca presentó efectos importantes en las comunidades de productores primarios; en general la biomasa de las comunidades asociadas al sedimento disminuyó significativamente con el aumento del tamaño de la cuenca. Debido a que el tamaño de las lagunas aumenta con el tamaño de las cuencas, es posible que esta relación indique un efecto de la turbulencia provocada por el viento y la hidrología, que es más importante en lagunas más grandes (Scheffer 1998, Kalff 2003), por lo que la superficie del sedimento no podría ser colonizada fácilmente por dichas comunidades. El fitoplancton en cambio, fue indiferente a este factor externo. Un efecto similar fue observado en un estudio de 18 pequeñas lagunas de agua dulce en Uruguay por Kruk *et al.* (2009).

Las plantas sumergidas mostraron una elevada variabilidad en las lagunas costeras de Uruguay, excepto en Laguna del Diario (Fig. 4, Cap. I). Estas plantas se encontraron presentes todo el año únicamente en Laguna de Rocha, aunque con importantes fluctuaciones de composición y biomasa, mientras que en las restantes lagunas con conexión al mar están ausentes la mayor parte del tiempo y presentan proliferaciones esporádicas. Dado que la Laguna de Rocha está sufriendo un proceso de eutrofización y que presenta importantes comunidades de plantas sumergidas se predijo que las mismas podrían estar aumentando debido al mayor aporte de nutrientes. Sin embargo, los resultados de esta tesis muestran que la abundancia de plantas sumergidas estaría más determinada por cambios en la salinidad (Tabla. 3, Cap. II), rechazando la predicción correspondiente, pero apoyando la predicción previa que postula que la conexión con el mar disminuye los indicadores de eutrofización, en este caso la abundancia de plantas sumergidas. En las lagunas costeras cohabitan especies de plantas sumergidas de sistemas de agua dulce, salobre e incluso marino, debido a la mezcla de masas de origen fluvial y marino. Las

especies muestran diferentes estrategias de vida entre las que se incluyen tolerancia a la salinidad y su variabilidad, producción de biomasa y reproducción sexual o asexual, entre otros. Aparentemente, algunas especies se expanden rápidamente cuando encuentran condiciones favorables de salinidad. Con salinidades altas se favorecen las especies tolerantes mientras que las de agua dulce se restringen en "áreas de refugio" en bahías límnicas o en desembocaduras de arroyos, pero cuando la barra se mantiene cerrada por largos períodos y la salinidad es baja estas especies se expanden a partir de propágulos y semillas y cubren grandes extensiones de la laguna. Cuando la salinidad aumenta debido a la conexión con el mar las plantas menos tolerantes reducen su abundancia nuevamente. Este fenómeno de proliferación de plantas sumergidas fue observado al menos dos o tres veces (en 1996 y 2001) en la Laguna de Rocha, pero fue registrado por un estudio sistemático por primera vez en 2003 (Rodríguez-Gallego *et al.* 2010).

Si bien los resultados indican que la salinidad es el factor principal que determina la fluctuación de la abundancia de las plantas sumergidas, no se descarta que un aumento de la carga de nutrientes favorezca dicha variabilidad, ya que la biomasa de plantas en las lagunas aumentó significativamente con la carga de nutrientes recibida desde la cuenca (Fig. 5, Cap. I). Si las condiciones de salinidad son las adecuadas y los nutrientes no son limitantes el proceso podría ser más rápido e intenso, debido a que las especies colonizadoras que desarrollan mayores biomásas se favorecerían. Por tanto, es esperable que en lagunas costeras de conexión obstruida enriquecidas en nutrientes se observen proliferaciones de plantas sumergidas seguidas de una rápida reducción, luego del cambio de salinidad. Este fenómeno aumentaría la variabilidad de los sistemas, ya que la dominancia temporal de plantas puede tener efectos sustanciales en procesos biogeoquímicos y la trama trófica, como sedimentación/resuspensión y refugio para especies de bentos y peces. El aumento de los nutrientes disponibles en conjunto con una alta variabilidad de la salinidad podría provocar, además de una alternancia de fases con y sin plantas, una alternancia de fases dominadas por macroalgas que se favorecen en períodos más salinos y de alta disponibilidad de nutrientes, o incluso por fitoplancton, promoviendo la ocurrencia de floraciones algales (McGlathery 2001; Rabalais 2002). Proliferaciones de macroalgas marinas, metafiton y fitoplancton han sido observadas al menos en la Laguna de Rocha en varias ocasiones.

El estudio de polen reciente en los sedimentos de las lagunas costeras que aún mantienen conexión con el océano permitió confirmar que las especies de plantas sumergidas están establecidas en las lagunas desde hace al menos 60-90 años, que incluso están presentes en lagunas donde los relevamientos botánicos no las habían registrado como en Laguna José Ignacio y que no existe un patrón de incremento de su abundancia en el tiempo (Fig. 2, Cap.

III). Estos resultados rechazan la predicción que establecía que las plantas sumergidas han colonizado recientemente estos ambientes y que su abundancia ha ido en aumento. Dicha predicción se estableció debido a la alta variabilidad de la abundancia de plantas sumergidas en todas las lagunas costeras, las proliferaciones esporádicas y su ausencia en Laguna José Ignacio, sumado a que el primer registro formal de estas especies en las lagunas costeras de Uruguay fue recién en 2001, esto fue interpretado *a priori* como una colonización reciente favorecida por una mayor disponibilidad de nutrientes. El registro polínico a su vez, no detectó proliferaciones de plantas, debido a que no se observaron picos de abundancia de granos de polen de plantas sumergidas, incluso en los sedimentos más recientes de la Laguna de Rocha donde al menos ocurrió una proliferación en 2003. Esto, más que indicar que las proliferaciones de plantas sumergidas son fenómenos recientes, indicaría que el registro polínico no es tan sensible como para detectarlas. Por el contrario, se observaron ausencias temporales en el registro de varias taxa de plantas sumergidas (Fig. 2, Cap. III), lo que estaría reflejando la alta variabilidad natural de esta comunidad. En el caso de la Laguna Garzón, se observó un aumento considerable en el polen de un taxa de planta sumergida hacia profundidades intermedias del sedimento. Esto podría deberse más que a proliferaciones a fases de varios años con dominancia de plantas sumergidas, intercalados con períodos sin plantas. Debido a que dicho taxa no es muy tolerante a salinidades elevadas, es posible que la proliferación se haya debido a un largo período de agua menos salobre, dado que esta es la laguna con la más baja frecuencia de conexión al mar. El mismo taxa se encuentra dominando la comunidad de plantas sumergidas en Laguna del Diario, indicando que el crecimiento puede ser una respuesta del sistema a períodos prolongados sin conexión al mar y tal vez a un aumento temporal de la carga interna de nutrientes, debido a la menor frecuencia de conexión.

Cambios en el régimen salino y estado trófico en las lagunas costeras de Uruguay han sido descritos a lo largo del Holceno por García-Rodríguez *et al.* (2004) e Inda *et al.* (2006). Estos autores encontraron consistentes aumentos del estado trófico de la Laguna de Rocha durante períodos de menor salinidad e influencia marina, en los cuales podrían haber fases dominadas por macrófitas. Esto indicaría que el funcionamiento natural de estos sistemas incluye la alternancia de fases de agua salobre y menor estado trófico y fases de menor salinidad y dominancia de plantas acuáticas. El registro de polen mostró a su vez, una rica composición de taxa de plantas terrestres y acuáticas que pudo ser asociada a su vez a las diferentes formaciones botánicas de las cuencas, contribuyendo además con futuros estudios paleoambientales de las lagunas costeras.

Planificación de los usos del suelo para minimizar conflictos socio-ambientales

El análisis multi-atributo y multi-objetivo realizado en esta tesis indicó que en el 4% de la cuenca de las lagunas costeras con conexión al mar se desarrollan actividades que son incompatibles entre sí y que al superponer los mapas del territorio apto para cada sector de usuarios (Agricultura, Turismo, Forestación, Ganadería extensiva y Conservación de la biodiversidad) la superficie de la cuenca apta para usos antagónicos aumentaría a 20.3%. Este análisis descartó la predicción que establecía que la interferencia entre usos actuales era elevada pero corroboró la segunda parte de dicha predicción que establecía que las interferencias aumentarían si los usos más intensivos continúan expandiéndose. Asimismo, se observó que los usos más intensivos y que presentan mayores incompatibilidades con los otros usos (agricultura y forestación), ocupan una muy baja proporción de sus suelos aptos (Fig. 2, Tabla 1, Cap. IV). Los usos que presentan mayor superposición entre sí y con relaciones antagónicas son principalmente agricultura, forestación y conservación de la biodiversidad. Estos resultados tienen varias implicancias desde el punto de vista del ordenamiento ambiental de las cuencas de las lagunas costeras. En primer lugar, si bien la superficie de la cuenca que actualmente presenta interferencias entre usos es baja, ha sido suficiente para generar conflictos entre sectores conservacionistas y productivos y el Gobierno, como se han observado en los últimos años. En segundo lugar, dado que los usos más intensivos como la agricultura y la forestación han ocupado una baja proporción de su territorio apto, y considerando la tendencia de intensificación de los mismos en la zona, es esperable que los conflictos entre sectores se incrementen considerablemente en el corto plazo. Si bien *a priori* se asume que los conflictos entre sectores serían mayoritariamente con el sector conservacionista, es posible que otros conflictos latentes podrían ser incluso más graves, como el reemplazo de usos tradicionales como la ganadería extensiva por usos más intensivos, o incluso la competencia por tierras entre forestación y agricultura.

La optimización de los usos del suelo para minimizar la eutrofización y la pérdida de biodiversidad, a la vez que maximizar la aptitud total del sistema, generó un mapa óptimo en que los diferentes usos se asignaron a los píxeles del territorio que presentan la mayor aptitud (Fig. 3, Cap. IV). Los usos antagónicos fueron eliminados, seleccionando a los que presentaron la mayor aptitud para ese píxel. De esta manera se cumplió con la predicción que establecía que la agrupación de los usos compatibles en las zonas correspondientes de mayor aptitud contribuye a minimizar los conflictos entre sectores de usuarios. En este sentido las herramientas multiatributo y multiobjetivo permitieron determinar las zonas de mayor aptitud para cada uso del suelo, analizar los conflictos entre usos antagónicos y proponer alternativas de ordenamiento que minimicen los conflictos entre usos que compiten por la tierra.

Los resultados obtenidos por esta metodología son útiles para guiar planes de ordenamiento territorial y analizar la situación actual y escenarios futuros. Sin embargo, su aplicación directa no es viable ni recomendable, ya que muchas actividades ya están implantadas a pesar que su inclusión no sea la ubicación más apta (Bojórquez-Tapia *et al.* 2001). Además, los diferentes propietarios tienen sus propios objetivos, valores y tradiciones, lo que no responde únicamente a la aptitud del suelo. Por el contrario, estos resultados ayudan a construir un mapa de ordenamiento ambiental ideal al que las políticas públicas podrían tender si buscasen maximizar el desarrollo económico a la vez que evitar conflictos ambientales y entre usuarios del suelo. Una fortaleza relevante de estas metodologías es que pueden diseñarse de manera de incorporar la participación pública (Malczewski 2006), aunque esto no fue explotado en este trabajo por exceder los objetivos de la tesis. Sin embargo, es un aspecto relevante a la hora de seleccionar herramientas para la elaboración de políticas públicas o de ordenamiento ambiental y territorial.

CONCLUSIONES Y RECOMENDACIONES GENERALES

Si bien las lagunas costeras son ecosistemas altamente dinámicos, la combinación de diferentes estrategias y metodologías de investigación permitieron evidenciar un proceso de eutrofización y los impactos de la alteración de la conexión natural con el mar, que si bien no han alcanzado niveles drásticos (exceptuando Laguna de Diario), ya presentan efectos en el funcionamiento de las mismas.

A excepción de la Laguna del Diario, las restantes lagunas costeras están recibiendo cargas moderadas de nutrientes desde la cuenca, las cuales se han incrementado principalmente en la última década. Pese a que los aportes no son tan elevados como en cuencas predominantemente agrícolas o urbanizadas, se evidencian efectos en los indicadores de eutrofización y se han observado respuestas del ecosistema como por ejemplo floraciones de cianobacterias.

Los usos que aportan mayor cantidad de nutrientes son la ganadería extensiva y la población humana, aunque en la última década se incrementó el aporte por las praderas artificiales y siembras en cobertura. La forestación no afectó a los indicadores de eutrofización, mientras que la agricultura mostró un claro aporte de sólidos en suspensión y una tendencia a aumentar el fósforo en las lagunas.

La conexión entre las lagunas y el mar afectó drásticamente los indicadores de eutrofización, disminuyendo sus valores con el aumento de la salinidad en el agua. En el caso de la Laguna del Diario, la obstrucción de la conexión con el mar, asociada a un aumento de la población en la cuenca en la última década, habrían disparado el proceso de eutrofización que presenta actualmente.

Si bien se observó que la abundancia de plantas sumergidas aumenta con la carga externa de nutrientes recibida desde la cuenca, las proliferaciones observadas en Laguna de Rocha y la alta variabilidad observada en todas las lagunas se explicarían por la variabilidad de la salinidad causada por la conexión con el océano. Un continuo incremento de los nutrientes, asociado a una alta variabilidad de la salinidad, podría generar alternancia entre productores primarios, ya sean plantas sumergidas, macroalgas marinas y fitoplancton, aumentando aún más la variabilidad del sistema.

Según el registro polínico en el sedimento reciente de las lagunas costeras que aún se conectan con el mar, las plantas sumergidas han estado presentes desde al menos 60-90 años y su abundancia habría sido muy variable en todo el período. Incluso, la Laguna Garzón podría haber desarrollado una fase dominada por plantas sumergidas, similar a la observada en Laguna del

Diario, pero posiblemente asociada a períodos prolongados de menor salinidad y baja conectividad con el océano.

El manejo artificial de la conexión entre las lagunas y el mar puede afectar el funcionamiento natural de las mismas, siendo la obstrucción de la conexión un impacto muy significativo. Pese a que los efectos de las aperturas artificiales no están claros y requieren mayores esfuerzos de investigación, se constató un efecto importante en la abundancia de las plantas sumergidas.

Al analizar la distribución espacial de los usos actuales y los mapas de aptitud para cada sector en la cuenca de las lagunas costeras, se observó que si bien los conflictos entre usos del suelo actualmente no afectan gran superficie, podrían hacerlo a corto plazo, generando nuevos conflictos socio-ambientales y agravando los ya existentes.

Pese a que se requiere mayor investigación sobre los procesos de transporte y de retención de nutrientes desde la cuenca a los cuerpos de agua, es posible hacer algunas recomendaciones generales para la gestión de los recursos naturales, que con bajo costo podrían minimizar la exportación de nutrientes. Estas son conservación y rehabilitación del bosque ripario en predios agropecuarios, incluyendo a los ganaderos extensivos, o evitar la canalización de humedales que pudiera acelerar el transporte de nutrientes a los cuerpos de agua. Estas medidas contribuirían además a conservar la biodiversidad.

Dado que la calidad ambiental de la zona no ha sido irreversiblemente afectada y que el grado de conflictividad entre sectores es incipiente, se recomienda en la zona aplicar metodologías de planificación territorial que permitan maximizar los usos del territorio minimizando conflictos. En tal sentido, las herramientas multiatributo y multiobjetivo aparecen como alternativas a las formas *ad hoc* empleadas hasta el momento en el país.

En el marco del cambio climático, por el cual se espera un incremento de la precipitación y una mayor variabilidad climática, y considerando la tendencia de cambios e intensificación de los usos del suelo, es esperable que la carga de nutrientes exportada a las lagunas continúe aumentando por acción de dichos factores externos. De esta manera es probable que aumenten los síntomas de eutrofización en las lagunas a través de proliferaciones de productores primarios. Así mismo, se incrementará la variabilidad natural de estos sistemas, siendo más complejo aún discriminar causas naturales de humanas.

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**Anexo I - Can ephemeral proliferations of submerged
macrophytes influence zoobenthos and water quality in
coastal lagoons?**

Lorena Rodríguez-Gallego, Erika Meerhoff, Juan M. Clemente & Daniel Conde

Can ephemeral proliferations of submerged macrophytes influence zoobenthos and water quality in coastal lagoons?

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Abstract Hydrology is often the main determinant of water chemistry and structure of the aquatic communities in coastal lagoons, driven by the interaction of freshwater load from the catchment and marine intrusions. However, submerged aquatic vegetation (SAV) can have important local effects on both features, even during sporadically and short proliferations. A SAV summer proliferation was observed during 2003 in a coastal lagoon in Uruguay (Laguna de Rocha), increasing macrophyte cover and biomass in the less saline zones. SAV summer proliferations were first observed in summer 2001, with no records prior. The aim of this paper is to describe the ephemeral proliferation of SAV in this shallow brackish lagoon and to analyze its effects on the abiotic environment and on the zoobenthic community. Vegetated and unvegetated zones were sampled in the northern more limnic area ($9.1 \text{ mS cm}^{-1} \pm 4.8$) and the southern brackish area ($20.9 \text{ mS cm}^{-1} \pm 5.2$). Water and sediment chemistry were analyzed by standard methods

and benthos and plants were collected with an Ekman grab. During SAV proliferation, suspended solids were five times lower inside macrophyte patches and water column total phosphorus and nitrogen were three and two times lower, respectively. Zoobenthos abundance and richness were higher in vegetated patches. However, no differences were found between sampling sites in the more brackish southern area and in the North after the SAV proliferation ended. This indicates that SAV can influence water chemistry and benthos structure above a biomass threshold of 100 g DW m^{-2} . Although hydrology is the driving force regulating communities and water chemistry in these coastal lagoons, our results showed that SAV can also be an important local factor above a certain biomass threshold.

Keywords Coastal lagoons · Submerged macrophytes · Structuring role · Benthos · Uruguay · Laguna de Rocha

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Introduction

Submerged aquatic vegetation (SAV) has a strong influence on the physical and chemical features of shallow lakes and also plays an important structuring role on biological communities (Moss, 1998; Scheffer, 1998). SAV can alter the oxygen and pH profiles in the water column (Frodge et al., 1990), as well as minimize water turbulence caused by wind and

currents (Scheffer, 1998 and references therein), preventing sediment resuspension (James et al., 2004; Moore, 2004). Submerged macrophytes can also attenuate eutrophication by stabilizing clear water states, outcompeting phytoplankton for nutrients and light, among other complex biological interactions (Scheffer, 1998; Søndergaard & Moss, 1998). Macrophytes act as a refuge for zooplankton (Timms & Moss, 1984; Mazzeo et al., 2003), crustaceans (Pérez-Castañeda & Defeo, 2004) and fishes (Stevenson, 1988; Jeppesen et al., 1998; Meerhoff et al., 2003). The benthic community shows a strong association with SAV (Thomaz et al., 2008), generally with higher richness and total abundance in vegetated than in unvegetated zones (Stevenson, 1988; Bergey et al., 1992; Connolly, 1997) due to the higher diversity of habitats, refuge and food availability (Diehl & Kornijów, 1998).

The effects of SAV are well known in marine (Green & Short, 2003) and freshwater systems (Scheffer, 1998) but have not been synthesized for brackish environments (Stevenson, 1988). Due to the higher variability of abiotic gradients (mainly light and salinity) and the hydrological regime in estuaries and coastal lagoons, diversity is generally lower than in more stable freshwater and marine environments. This is the case for submerged macrophytes (Stevenson, 1988) and for benthos (Remane & Schlieper 1971; Attrill 2002). However, the general role of SAV is expected to be similar under similar biomass and cover conditions in freshwater, brackish, and marine systems since the major effects seem to be related to its role in increasing the structure of waterscapes (James et al., 2004; Meerhoff et al., 2007a, b; Thomaz et al., 2008).

Coastal lagoons are characterized by large hydrological dynamics driven by the connection with the ocean, which determines steep salinity gradients (Kjerfve, 1994; Suzuki et al., 1998; Chagas & Suzuki, 2005). It is well known that abiotic gradients determine the structure of biological communities in coastal lagoons (Kjerfve, 1994). In Laguna de Rocha (Atlantic coast of Uruguay, South America), hydrology and physicochemical gradients determine phytoplankton (Bonilla et al., 2005), phytobenthos (Conde et al., 1999), bacteria (Piccini et al., 2006) and zoobenthos abundance and composition (Pintos et al., 1991). At this lagoon, SAV is confined to shallower areas and small bays protected from strong coastal

winds. A previous stable isotope study (Rodríguez-Graña et al., 2008) showed that direct consumption of SAV by herbivores was low as well as the SAV relative contribution to detritus. However, zoobenthos was found to play a key role in the transfer of energy to higher trophic levels (Rodríguez-Graña et al., 2008). Arocena (2007) also found an increase in species richness and abundance in a small and dense vegetated bay within the limnic area, compared to unvegetated sites. However, these results cannot be extrapolated to other zones of the lagoon where conductivity and SAV biomass are different.

Periodically, an increase in biomass and cover of SAV has been observed in summer in Laguna de Rocha, in the northern and more limnic areas, which commonly lasts until Fall. This phenomenon was first observed in 1997, 2001 and also during this study in March 2003 when it attained the maximum magnitude. No reports of similar phenomenon in other coastal lagoons of the region are available. The causes of these periodic and ephemeral proliferations of SAV are not known yet, although an incipient eutrophication process is hypothesized (Aubriot et al., 2005) due to land use intensification in the basin during the last decade (Rodríguez-Gallego et al., 2009). However, climatic factors cannot be discarded, since rainfall increased 20% in Uruguay mainly after 1970 (Bidegain et al., 2006) and in the region (Bates et al., 2008) affecting coastal zones due to increased runoff (Genta et al., 1998). Under this scenario, SAV ephemeral dominance could increase in frequency and duration, imposing unexpected long-term effects on water quality and on the food web structure. Furthermore, SAV proliferations could become frequent in other coastal lagoons of the region, probably with similar consequences in the functioning of the system.

The coastal zone and estuaries are highly impacted by eutrophication (Nixon, 1995; Rabalais, 2002) and SAV development could be one of its main consequences. Due to the important structuring effects of macrophytes in shallow systems functioning, understanding SAV dynamics and its effects on water quality and biological communities is crucial to recommend management practices in coastal lagoons. The aim of this paper is to describe an ephemeral proliferation of SAV in the shallow brackish Laguna de Rocha (Uruguay) and analyze its effects on the abiotic environment and on the zoobenthic community.

Materials and methods

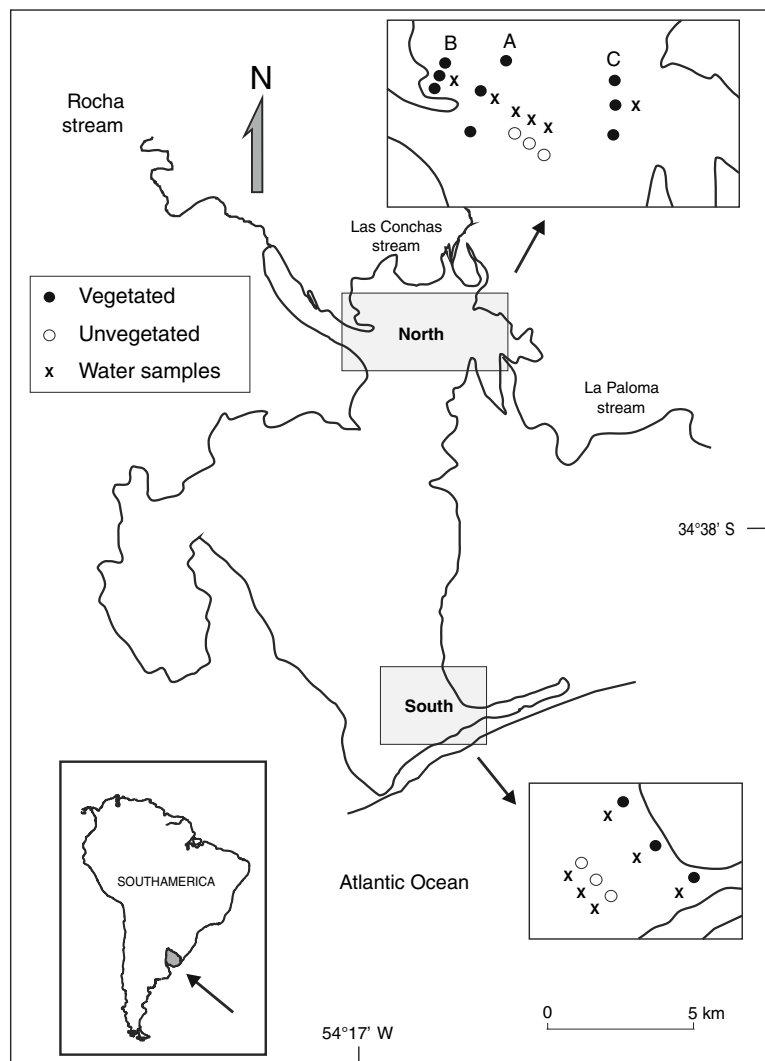
Study area

Laguna de Rocha constitutes a nursery and reproductive area for important regional fish resources (Fabiano et al., 1998; Vizziano et al., 2002; Norbis & Galli, 2004) and for resident and migratory aquatic birds (Morrison et al., 1989; Aldabe et al., accepted). The lagoon was declared a Lacustrine National Park in 1977, is included in the MaB-UNESCO Reserve “Bañados del Este” and has been proposed as a new Ramsar site in Uruguay. It is currently being inducted into the National System of Natural Protected Areas

and therefore represents a relevant site for current conservation efforts.

Laguna de Rocha (Rocha, Uruguay; $34^{\circ}38' S$ – $54^{\circ}17' W$) (Fig. 1) has a surface area of 72 km^2 and an average depth of 0.6 m. It periodically connects with the Atlantic Ocean through a channel that opens through the sandbar (Pintos et al., 1991). The connection generally occurs two to four times a year and causes steep salinity variations. Therefore, hydrology is the driving force for the functioning of the whole ecosystem, due to the periodic interaction of water masses of limnic and marine origin (Conde et al., 2000, 2002; Bonilla et al., 2005; Giménez et al., 2005). The lagoon shows large hydrodynamics,

Fig. 1 Map of Laguna de Rocha indicating the sampling points. The sampling zones (A, B, C, and South, both vegetated and unvegetated) are indicated. Crosses represent water samples for nutrient analysis and circles represent biological samples (*black circles* indicate vegetated zones and *open circles* unvegetated zones)



but the sediments are always flooded. Biota, from bacteria to birds, are adapted to salinity fluctuations, alternating between freshwater, brackish and marine species both in time and space. Bonilla et al. (2006) summarized 20 years of biological and physicochemical data for this lagoon, although SAV recording started after 2001. The connection with the ocean is often artificially performed by the local municipality to reduce flooding and allow commercial fish and crustaceans larvae to enter the system. Nevertheless, no impact assessment of this modification exists (Conde & Rodríguez-Gallego, 2002). Although monitoring is performed, no long-term standardized assessment of the sand bar opening dynamics is available.

In March 2003, an abundant proliferation of SAV was observed expanding from the outlet of the tributaries and small bays to the central pelagic zone. SAV reached the water surface, allowing a clear view of the limits, observed during a preliminary survey from a light aircraft. Three main zones were arbitrarily defined by direct observation during the flight: (1) an open water zone without SAV, in the center of the northern area; (2) a shoreline zone composed of small bays with *Spartina densiflora* and showing the highest abundance of SAV; and (3) a larger intermediate zone, with lower SAV abundance.

Sampling design and estimation techniques

A flight on a light aircraft was conducted in March 2003 to qualitatively evaluate the expansion of SAV cover and to assist design of a representative sampling strategy. Sampling was designed to account for the variability of all the zones. The bay zones (referred as zone B hereafter) were so shallow during March 2003 ($Z < 0.1$ m) that sampling points had to be taken close to each other (< 200 m). The intermediate zone, dominated by *P. pectinatus*, was divided in two subzones due to its extent: the area influenced by the outlet of Rocha stream (zone A hereafter) and the area influenced by the outlet of both La Paloma and Las Conchas streams (zone C hereafter) (Fig. 1). A southern vegetated zone near the sand bar was also included to integrate the whole salinity gradient of the lagoon. In both the North and South areas, unvegetated zones were also sampled (Fig. 1).

Sampling was conducted in March 2003, December 2003, and February 2004 at each zone in the North

(A, B, C, and unvegetated) and South (vegetated and unvegetated). SAV cover was not quantified. Triplicate random samples were taken with an Ekman grab, collecting macrophyte biomass (above and below ground) and zoobenthos, following the method of Arocena (2007). When plants reached the water surface, the grab was carefully handled to avoid material loss. Plant biomass and benthic organisms were separated under constant water flux on a 1 mm^2 mesh screen. Plants were separated by taxa and dry weight was estimated after 48 h in a drying oven at 80°C , without discriminating above and below ground biomass. Total SAV biomass (TB) was calculated as the sum of individual species biomass. Zoobenthos organisms were fixed with 10% formalin. Macrofauna were hand sorted from coarse sand and detritus and preserved in 70% alcohol. The abundance of organisms, identified to the species level when possible, was determined for each sample. In situ parameters were also measured in triplicate with field sensors, at the same sampling points. The parameters measured were depth (Z), pH, and conductivity (K ; Horiba D-24 sensor), photosynthetically active radiation (PAR) to derive PAR attenuation coefficient (K_{dPAR} ; 400–700 nm) (LI-COR LI 250 sensor), temperature, and dissolved oxygen (T and DO; Horiba D-25 sensor). Precipitation data of the Rocha Station were obtained from the National Meteorological Service. The state of the sand bar (open or closed) was visually inspected on each sampling occasion.

Water samples were collected at ca. 10 cm depth with a Ruttner bottle (after verifying complete mixing of the water column by checking temperature and conductivity every 20 cm) and were later analyzed for total and organic suspended solids (SS and OM, respectively; APHA, 1985), ammonium (NH_4 ; Koroleff, 1970), nitrite (NO_2 ; Strickland & Parsons, 1972), nitrate (NO_3 ; Mackereth et al., 1978), total nitrogen (TN; Mackereth et al., 1978), soluble reactive phosphorus (SRP; Murphy & Riley, 1962), total phosphorus (TP; Valderrama, 1981) and reactive silica (RS; Müllin & Riley, 1955). Sediment samples were manually collected down to a depth of 2 cm using an acrylic corer (5 cm in diameter). The organic content of the sediment was determined by ignition (OMsed; APHA, 1985) and TN (TNsed) and TP (TPsed) according to Valderrama (1981). Triplicate water and sediments samples were taken at the

South and unvegetated northern zones, while single samples were taken at A, B, and C zones and considered replicates of the northern vegetated zone.

Data analyses

Two-way ANOVAs were conducted to determine differences in abiotic variables among vegetated and unvegetated zones, independently for North and South areas. Also, two-way ANOVAs were used to test differences in time and space (all sampling sites) for TB, SAV richness, benthos abundance, and richness. Parametric assumptions were tested by Bartlett and Cochran tests and normality by Kolmogorov–Smirnov test. $\text{Log}(x + 1)$ and square root were used to transform the tested variables when necessary to fulfill normality and homocedasticity assumptions (Zar, 1999). Spearman correlations were also used to determine linear relationships between species and environmental variables. Canonical correspondence analysis (CCA) was used to analyze the relationship between macrophytes species biomass and environmental variables as explanatory variables. A redundant analysis (RDA) was conducted to analyze the relationship between zoobenthos abundance as dependent variables with environmental and SAV as explanatory variables. The selection of the type of analysis was determined according to the length of the data gradient after a preliminary detrended analysis (ter Braak & Smilauer 1998; Lepš & Šmilauer, 2003). Both for CCA and for RDA analyses, the selection of explanatory variables was made using the CANOCO 4.52 manual selection option and the variables with a $P < 0.1$ of the Monte Carlo Permutation Test and variation inflation factors (VIF) values lower than 20 were retained. The significance of the first axis and all the axes of the RDA and CCA was tested with permutation tests. Groups of samples identified in the RDA were tested for all variables together using the Kruskal–Wallis nonparametric Test. An RDA variance partitioning procedure was used following Borcard et al. (1992) and Peeters et al. (2004) to quantify the relative contribution of the explanatory variables to the explained variance. Explanatory variables were separated in two groups, and to determine the variance explained by the first group the variables of the second one were removed from the analysis, selecting them as covariables. The inverse procedure was

conducted to determine the variance explained by the second group of explanatory variables. Data analyses were conducted using PAST 1.71 (Hammer et al., 2001) and CANOCO for Window 4.52 (Biometrics, 1997–2003).

Results

Spatial and temporal environmental dynamics

Prior to the first sampling in March 2003, the lagoon was isolated from the ocean at least since October 2002. It was artificially opened a few days prior to the first sampling, allowing the lagoon to discharge freshwater into the ocean. Afterward, a saline intrusion into the estuary occurred, reaching the unvegetated and C zones in the North, during the first sampling period. Freshwater conditions were maintained in zones A and B. The sand bar remained open until November 2003 and closed naturally before the December 2003 sampling. It remained closed until February 2004, although brackish conditions were maintained in the system mainly due to summer evaporation and low precipitation. Precipitation accumulated 30 days before each sampling was maximum in December 2003 (180 mm) and minimum in March 2003 (62 mm).

Oxygen saturation was always observed, without differences between surface and bottom. Mean water temperature for the three sampling sessions was $23.4 \pm 2.2^\circ\text{C}$ (Table 1). Z showed a wide variation (0.3 m in March 2003 to 1.7 m in December 2003), being always higher in the South and in unvegetated zones (Table 1). pH was close to neutrality (7.6 ± 0.45), increasing slightly toward the northern vegetated areas. Even K was highly variable (3.6–29.6), a gradient was observed decreasing from South to North. In northern stations, K was significantly higher in the unvegetated (Table 1) and C zones, while the zone B always had lower values (data for the northern vegetated zones were averaged for presentation in Table 1). RS showed an opposite pattern to K (Table 1) with a negative significant correlation ($R = -0.78$, $P < 0.005$). K_{dPAR} and SS were generally higher in the North, mainly during SAV proliferation in March 2003 (Table 1). K_{dPAR} was significantly higher in B while SS was higher at the unvegetated zone in the North, and the inverse

Table 1 Mean and standard deviation (in brackets) of water and sediment physicochemical variables in vegetated and non vegetated zones of Laguna de Rocha

Z (m)	K (mS cm ⁻¹)	K _{APAR} (m ⁻¹)	SRP (μg l ⁻¹)	TP (μg l ⁻¹)	DIN (μg l ⁻¹)	TN (μg l ⁻¹)	RS (mg l ⁻¹)	SS (mg l ⁻¹)	OMsed (%)	TPsed (μg g DW ⁻¹)	TNsed (μg g DW ⁻¹)
March 2003											
South vegetated	0.6x (0.2)	28.5 (1.1)	1.0 (0.2)	mv	mv	mv	mv	mv	16.3 (7.5)	70.8 (50.2)	mv
South unvegetated	0.9x (0.0)	25.4 (0.0)	1.7 (0.0)	0.0 (0.0)	20.2 (0.0)	485.3 (0.0)	1943.4 (0.0)	36.7 (0.0)	15.0 (4.0)	69.2 (20.2)	mv
North vegetated	0.3* (0.2)	7.4* (6.7)	7.6* (3.1)	0.0 (0.0)	26.5 (36.4)	358.5* (224.2)	3613.5 (260.0)	24.6* (8.6)	83.0 (76.2)	381.8 (343.3)	mv
North unvegetated	0.6* (0.0)	10.1* (3.2)	7.9* (0.8)	0.0 (0.0)	233.9* (36.2)	751.8* (113.0)	3761.8 (281.6)	130.9* (6.5)	21.7 (7.4)	176.0 (12.3)	mv
December 2003											
South vegetated	mv	mv	18.8 (3.1)	71.0 (9.1)	24.7 (5.8)	908.8 (168.8)	2270.3 (316.4)	40.8x (1.9)	8.0 (2.6)	65.2 (6.4)	51.2 (36.3)
South unvegetated	0.0 (0.2)	17.0 (0.0)	2.3 (0.0)	60.6 (0.0)	93.3 (0.0)	807.8 (0.0)	2126.5 (0.0)	35.0x (0.0)	9.0 (2.6)	67.1 (33.9)	21.4 (12.9)
North vegetated	0.9* (0.1)	7.2* (4.0)	3.0* (0.9)	24.4 (10.6)	47.2 (16.2)	622.0* (28.3)	3047.5 (703.0)	27.6* (9.5)	12.3 (9.3)	80.3 (27.6)	68.4 (83.7)
North unvegetated	1.3* (0.0)	10.1* (0.1)	2.2* (0.2)	16.4 (0.8)	31.2 (11.1)	813.0* (92.6)	2693.3 (238.1)	22.4* (2.2)	18.3 (4.0)	102.6 (22.0)	40.8 (32.9)
February 2004											
South vegetated	0.7x (0.1)	19.3 (0.7)	2.1 (0.4)	18.7 (3.2)	79.1 (15.4)	723.6 (167.0)	925.5 (191.0)	32.3x (8.1)	9.3 (3.2)	73.3 (26.1)	32.5 (52.4)
South unvegetated	1.7x (0.0)	20.3 (0.0)	1.6 (0.0)	27.7 (0.0)	39.0 (0.0)	582.5 (0.0)	2217.7 (0.0)	22.3x (0.0)	6.7 (2.3)	100.9 (7.8)	43.9 (25.8)
North vegetated	0.8* (0.1)	10.3* (4.0)	1.4* (0.4)	19.6 (4.1)	21.8 (3.4)	629.1* (131.2)	3107.5 (328.5)	28.1* (18.5)	16.7 (9.1)	118.9 (90.2)	127.7 (94.8)
North unvegetated	1.1* (0.0)	14.2* (0.8)	1.1* (0.4)	24.8 (3.6)	24.6 (7.8)	630.4* (161.4)	2582.2 (195.4)	66.5* (4.5)	11.3 (2.5)	129.0 (33.1)	50.8 (49.0)

For Z, K, and K_{APAR} of the northern vegetated zones a mean value of zones A, B, and C is shown; mv: missing value. Significant differences (two way ANOVA, $P < 0.05$, F values are omitted) between vegetated and non vegetated zones are indicated separately for South (x) and North (*). See "Materials and methods" section for the acronyms description

pattern was significant in the South area (Table 1). Dissolved nutrients (SRP and dissolved inorganic nitrogen forms—DIN) showed no spatial pattern, fluctuating between samplings. TP and TN were significantly different between vegetated and unvegetated zones but only in the North, being higher in open waters mainly during SAV proliferation in March 2003 (Table 1). TP was positively correlated with SS ($R = 0.54$, $P < 0.005$) and K_{dPAR} ($R = 0.67$, $P < 0.005$). SS ($R = -0.79$, $P < 0.001$), TP ($R = -0.69$, $P < 0.001$), and TN ($R = -0.69$, $P < 0.001$) were negatively correlated with TB in the northern vegetated zone only in March 2003. OM_{sed}, TN_{sed}, and TP_{sed} were higher in the northern areas (Table 1), and were significantly correlated between them ($R > 0.55$, $P < 0.005$ in all cases). OM_{sed} was negatively related with K ($R = -0.69$, $P < 0.005$).

Community structure and distribution of submerged macrophytes

SAV community was composed of eight species: *Zannichellia palustris* L., *Ruppia maritima* L., *Potamogeton pectinatus* L., *Potamogeton pusillus* L., *Eleocharis nana* aff. Kunth, *Myriophyllum quitense* HBK, and two species of Charophytes, *Chara* sp. and *Nitella* sp., which were considered together. All the species were submerged except *M. quitense*, which had an amphibian life form with emergent tips, generally with flowers. Only in March 2003 did some individuals of *R. maritima* and *Z. palustris* have flowers and fruits. A richness pattern inverse to the K gradient was evident, being significantly different between sampling stations ($F_{(3,24)} = 8.12$, $P < 0.01$). While southern vegetated zones showed up to three taxa, the northern vegetated sampling sites reached the maximum richness (8 taxa), without significant differences between A, B, and C zones (Fig. 2A).

TB showed a similar pattern than richness, with maximum values during SAV proliferation in March 2003 ($F_{(2,24)} = 12.84$, $P < 0.001$) and in the B zone ($F_{(3,24)} = 4.91$, $P < 0.05$) (Fig. 2B). The maximum value of TB was 307.2 g DW m⁻² in the B zone during SAV proliferation and 20.3 g DW m⁻² in the South also in March 2003. In December 2003 and February 2004, in the zones A and C, TB decreased to <10% of the value observed in the March 2003 SAV proliferation, while in zone B TB decreased to half of

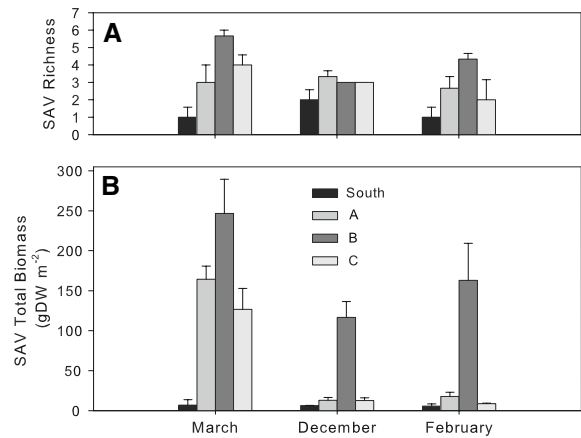


Fig. 2 Mean and standard error of SAV richness (A) and total biomass (B) in the four vegetated zones in Laguna de Rocha during the study period

its value. On the contrary, in the South TB was similar throughout the study period (Table 2).

A CCA (Fig. 3) with SAV species biomass as dependent variables and physicochemical variables as explanatory clearly differentiated the zone B samples from the others. The zone B samples were dominated by *M. quitense* and *Eleocharis* sp., with high values of sediment nutrients, precipitation and RS and low values of pH and K . The rest of the samples were associated to higher pH values but arranged along the K gradient. Generally, southern samples had higher *Z. palustris* biomass and K values, while zones A and C were associated with *R. maritima*, *P. pusillus*, and lower K values. Although zones A and C samples were basically grouped together and southern samples grouped apart, a considerable amount of dispersion of the samples along the K gradient was observed. This analysis explained 81.3% of the species variance both permutation tests were significant ($P < 0.002$).

Community structure and distribution of benthos

The zoobenthos community comprised 25 taxa. The maximum richness was found during the SAV proliferation in March 2003 ($F_{(2,36)} = 21.72$, $P < 0.001$) in zone B (11 taxa) followed by zone A (10 taxa) and the southern stations (8 taxa) ($F_{(5,36)} = 5.33$, $P < 0.01$) (Fig. 4A). Only during the SAV proliferation, richness was higher in the northern areas than in the South in vegetated zones, both in South and North areas. In December 2003 and

Table 2 Mean and standard deviation (between brackets) of SAV species biomass (above and below ground biomass were not discriminated) and TB (g DW m⁻²) in all vegetated sampling zones of Laguna de Rocha throughout the study period

	<i>Z. palustris</i>	<i>R. maritima</i>	<i>P. pectinatus</i>	<i>Eleocharis</i> sp.	<i>P. pusillus</i>	Characeas	<i>M. quitensis</i>	TB
March 2003								
South	0.8 (0.7)	6.1 (6.1)						6.9 (6.8)
A		55.2 (28.0)	37.3 (20.6)		9.3 (9.1)		9.3 (8.8)	164.3 (16.4)
B		15.1 (6.0)	27.0 (13.6)	65.6 (13.9)	2.7 (0.1)		88.2 (68.5)	246.7 (42.8)
C	10.1 (6.5)	2.7 (1.1)	73.0 (27.0)			0.4 (0.2)	0.1 (0.1)	126.7 (26.2)
December 2003								
South	1.5 (0.8)	4.7 (1.1)				0.1 (0.1)		6.2 (0.3)
A	0.7 (0.7)	3.5 (2.1)	3.0 (1.4)		0.9 (0.9)	0.1 (0.1)	0.4 (0.4)	12.9 (3.6)
B		0.8 (0.8)	0.9 (0.5)	48.6 (27.2)			40.2 (20.3)	116.6 (19.7)
C		4.3 (0.7)	3.3 (1.4)			1.2 (0.4)		12.5 (3.5)
February 2004								
South	2.3 (2.3)	3.3 (2.3)						5.6 (2.8)
A		10.6 (6.7)	0.5 (0.3)	0.1 (0.1)		0.2 (0.2)		17.8 (5.3)
B	0.3 (0.3)	1.6 (1.6)	4.4 (2.5)	45.4 (34.9)		0.4 (0.3)	80.2 (40.4)	162.9 (46.5)
C	0.1 (0.1)	3.5 (1.8)	2.0 (1.5)			0.1 (0.1)		8.8 (0.6)

TB Total biomass

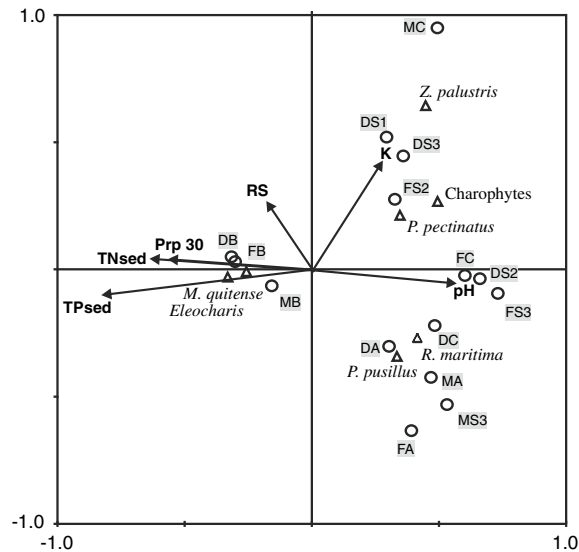


Fig. 3 CCA with SAV species biomass as dependent variables (triangles) and physicochemical variables as explanatory (bold arrows), for Laguna de Rocha during the study period. See methods for the selection of the explanatory variables. The sample labels indicate the month of the sampling and the sampling zone. M: March 2003, D: December 2003 and F: February 2004. S: South, A, B, and C indicate vegetated zones of the North

February 2004 richness was higher in the South but differences among vegetated and unvegetated zones were not significant.

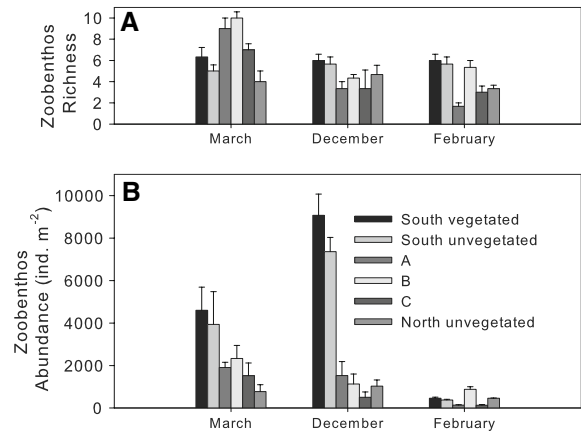


Fig. 4 Mean and standard error of zoobenthos richness (A) and total abundance (B) of all sampling zones in Laguna de Rocha during the study period

The zoobenthos assemblage comprised two species of mollusks, four crustaceans, four polychaetes, one collembola, and 14 insecta, from which eight species were chironomids. Five species were present in both North and South but generally with lower frequency in the northern area: *Nephtys fluviatilis* Monro (98%), *Dies fluminensis* Mañe-Garzón (60%), *Heteromastus similis* Southern (51%), *Sinelobus standfordi* Richardson (50%), and *Chasmagnathus granulata* Dana (21%). Four species were only present in the southern area: *Heleobia* spp. (25%),

Erodona mactroides Daudin (13%), collembola (1%), and *Cyrtograpsus angulatus* Dana (10%). The rest of the taxa were exclusive to the northern area, mainly during SAV proliferation in March 2003, with a frequency from 1 to 17%: Amphipoda, *Laeronereis culvieri* Webster, *Dicrothendipes* spp. (two taxa), *Goeldechironomus* sp., *Polypedilum* sp., *Chironomus* sp., *Rheotanytarsus* sp., *Cladotanytarsus* sp., *Larsia* sp., Oecophoridae, *Baetis* sp., *Caenis* sp., *Ocetis* sp., Leptocereidae (Atanotolico), and *Aganon* sp.

Zoobenthos abundance (Fig. 4B) was higher in the South than in the North ($F_{(5,36)} = 21.74$, $P < 0.001$) but differences between vegetated and unvegetated zones were not detected. The maximum abundance of the system was achieved in December 2003 (10273.8 ind. m⁻²) and March 2003 (6381.7 ind. m⁻²) both in the South ($F_{(2,36)} = 50.56$, $P < 0.01$). When analyzing the North separately, the maximum abundance of benthos was observed in March 2003 and December 2003 ($F_{(2,24)} = 13.82$, $P < 0.001$) (Fig. 4B). The B zone exhibited the maximum abundance of zoobenthos ($F_{(3,24)} = 3.66$, $P < 0.05$) during the March 2003 SAV proliferation and in February 2004 (Fig. 4B). The spatial pattern changed every sampling, but the differences among vegetated and unvegetated zones were less steep after March 2003 in the North. Total benthos abundance was positively correlated with TB only during the SAV proliferation, in March 2003 ($R = 0.68$, $P < 0.001$).

The most abundant zoobenthos species was *Heleobia* spp. in southern stations (Table 3), ten times higher than any of the other species. *N. fluviatilis* was the second most abundant species, followed by *D. fluminensis* and *H. similis*. The most important change in the community structure was the disappearance in December 2003 and February 2004 of most of the insect larvae that were abundant in the northern vegetated zones during the SAV proliferation, in March 2003. The total abundance of these species decreased from 298 ind. m⁻² (± 38) in March 2003 to 0 and 4 ind. m⁻² (± 1) in December 2003 and February 2004, respectively.

An RDA (Fig. 5) was conducted with the abundance of all benthos species, total benthos abundance and richness as dependent variables and the explanatory variables retained by the forward procedure and low VIF (T , K , TN , NH_4 , RS , $TPsed$, $OMsed$, *M. quitense*, *Eleocharis* sp., *P. pectinatus*, and *R. maritima*). This analysis explained 54.5% of the

species variance, and both permutation tests were highly significant ($P < 0.001$). The first axis represented the SAV and K gradient and the second one the total benthos abundance. The RDA discriminated three groups of samples. The most notable one grouped the northern vegetated samples mainly from the March 2003 SAV proliferation, with higher zoobenthos richness and insects as the dominant taxa. This group had higher TB, $OMsed$, $TPsed$ and RS and lower levels of K , TN , NH_4 , and T . At the opposite side of the gradient, a typical estuarine macrozoobenthos assemblage was found and samples were separated into two groups: one with southern samples with higher total zoobenthos abundance and another one with lower zoobenthos abundance which grouped with northern unvegetated samples and A, B, and C samples of February 2004 and December 2003. The three groups of samples were statistically different [overall value of the Kruskal–Wallis test: $H(2, N = 2049) = 57.97$, $P < 0.001$].

The variance partitioning procedure was conducted grouping the selected explanatory variables in: (1) SAV-related variables (*Eleocharis* sp., *P. pectinatus*, *R. maritima*, *M. quitense*, $OMsed$, and $TPsed$) and (2) hydrology-related variables (K , T , TN , NH_4 and RS). The variance explained by the SAV related variables was 42.1% and by hydrology related variables 26.2%, while the shared explained variance was high (31.7%). Both partial RDA had significant Monte Carlo Permutation Tests.

Discussion

In this study, we found that when the ephemeral proliferation of SAV occurred, several changes in the physicochemical characteristics and biological communities of Laguna de Rocha took place. SAV promoted the reduction of total nutrients of the water due to the decrease in water turbulence and sediment resuspension, as well as acting as a trap for suspended solids. Furthermore, SAV increased the spatial heterogeneity and offered habitat for zoobenthos species, promoting the increase of benthos richness and abundance.

Vegetation description and SAV proliferation

SAV in Laguna de Rocha was composed by the typical association of brackish systems species,

Table 3 Zoobenthos abundance (ind. m⁻²) of the most frequent taxa (frequency higher than 10%)

	<i>N. fluviatilis</i>	<i>S. stanfordi</i>	<i>D. fluminensis</i>	<i>H. similis</i>	<i>Ch. granulata</i>	<i>E. mactroides</i>	<i>Heleobia</i> spp.	<i>C. angulatus</i>
March 2003								
South vegetated	384 (80)	225 (304)	60 (28)	258 (172)		20	2569 (2783)	20 (0)
South unvegetated	172 (109)	212 (267)	99	179 (124)	2	30 (14)	1610 (1172)	
A	58 (30)	5 (2)	60 (20)	5 (4)				
B	35 (28)	7 (2)	103 (83)	2				
C	41 (8)	21 (14)	17 (6)	5 (3)				
North unvegetated	51 (31)	4 (1)	6 (3)	8 (7)				
December 2003								
South vegetated	312 (70)		305 (144)	219 (190)	33 (23)	40 (0)	5465 (4112)	40
South unvegetated	298 (72)		239 (182)	113 (30)	212 (191)	20	6488 (1274)	20
A	52 (14)	63 (57)	31 (35)	17 (21)				
B	24 (9)	77 (83)	4 (0)	5 (4)				
C	16 (18)	7 (7)	4 (4)	4				
North unvegetated	28 (4)	21 (15)	24 (0)	14 (0)				
February 2004								
South vegetated	16 (4)		9 (9)	8 (11)	2 (1)	2 (0)	411 (74)	2
South unvegetated	15 (4)		9 (11)	6 (2)	11 (10)	1	326 (64)	1
A	12 (4)	2 (0)						
B	19 (15)	3 (1)	47 (22)		10 (11)			
C	6 (3)	4 (0)	3 (1)					
North unvegetated	35 (1)	2 (0)	2 (0)	8 (0)				

Standard deviation is indicated in brackets

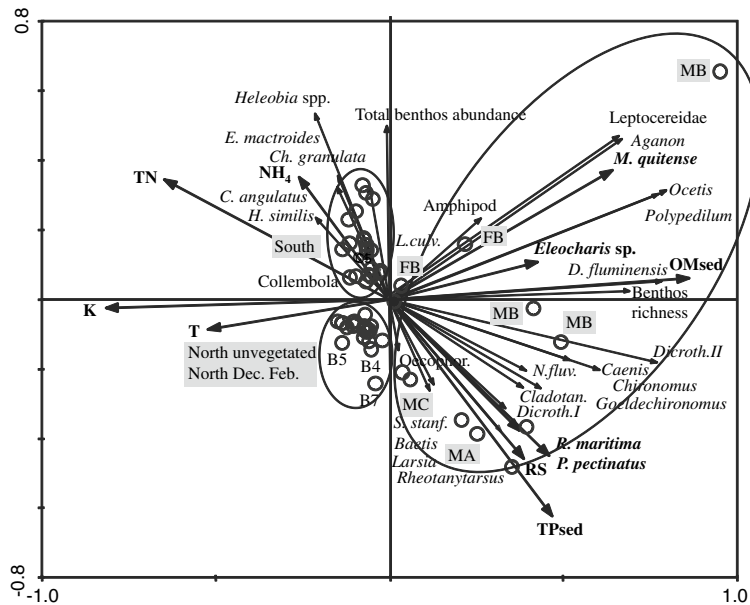


Fig. 5 RDA with the abundance of all benthos species, total benthos abundance, and richness (arrows) of all sampling zones in Laguna de Rocha during the sampling period. The explanatory variables (bold arrows) were T, K, TN, NH_4 , RS, TPsed, OMsed, *M. quitense*, *Eleocharis* sp., *P. pectinatus*, and *R. maritima*. See methodology for the selection of the explanatory variables. The samples labels (in gray) indicate

the month of the sampling and the sampling zone. M: March 2003, D: December 2003, and F: February 2004. S: South, A, B, and C indicate vegetated zones of the North. *L. culv.*: *L. culvieri*, Oecopher.: Oecophoridae, *S. stanf.*: *S. stanfordi*, *N. fluv.*: *N. fluviatilis*, *Cladotan.*: *Cladotanytarsus* sp., *Dicroth. I*: *Dicrothendipes* sp. I, *Dicroth. II*: *Dicrothendipes* sp. II

namely *Ruppia maritima*, *Zanichellia palustris*, *Potamogeton pectinatus*, and Charophyta (Kautsky, 1988; Kantrud, 1991). Also *Myriophyllum quitense* and *Eleocharis* sp. were present. Laguna de Rocha showed a higher richness of submerged plants than Lagoa dos Patos in Brazil (Seeliger, 1998) and Mar Chiquita in Argentina (Bortolus et al., 1998), but the biomass was generally lower. Unlike other coastal lagoons of Uruguay, in this lagoon plants are present the whole year and cover a large proportion of the shallower areas (Bonilla et al., 2006).

The SAV distribution was determined by reactive silicate, precipitation, conductivity, and sediment total phosphorus and total nitrogen. Semi-enclosed bays harbored more diverse and abundant SAV communities, as found in the zone B. This environment has the lower conductivity and maximum values of nutrients associated with sediments, due to the direct influence of freshwater discharge from the fluvial system, as indicated by higher reactive silicate concentrations and precipitation. SAV species were distributed according to their environmental

preferences and salinity tolerance. At southern stations, only highly salinity tolerant species were present (e.g., *Z. palustris* and *R. maritima*; Kantrud, 1991), while toward northern stations lower salinity tolerant species, such as *M. quitense* (Orchard, 1981; Ritter & Crow, 1998) and *P. pectinatus* (Kantrud, 1990; Schütz Rodrigues & Irgang, 2001), were found. *Ruppia maritima* is the angiosperm with the highest tolerance to salinity fluctuations (Murphy et al., 2003), which explains its large distribution in Laguna de Rocha.

Minor differences in abundance and composition among A, C, and southern vegetated zones, but great differences with B zone indicate that other factors may be involved and counteract the spatial heterogeneity driven by the conductivity gradient. Water turbulence caused by coastal winds could explain the restricted distribution of *M. quitense* to the protected zone B in contrast with other northern offshore stations with similar conductivity values (zones A and C). *Myriophyllum quitense* has highly segmented leaves which commonly occupies all water column and also has tips above the water surface (Orchard,

1981), which make them vulnerable to high turbulence (Sculthorpe, 1967; Cronk & Fennessy, 2001).

SAV biomass showed larger fluctuations in northern stations, reaching the maximum values in March 2003. During this sampling, *P. pectinatus* reached the water surface, covering a substantial part of the zones A and C of Laguna de Rocha. Similar values of SAV biomass were not observed during the following summers (Rodríguez-Gallego pers. obs.). The cause for this ephemeral proliferation of SAV is still not clear and no similar records were reported for the region. Possibly, plants grew rapidly in response to the favorable early summer conditions. Before March 2003 sampling, the lagoon was isolated from the sea. Although we have no summer records previous to our sampling in March 2003, probably low conductivity, intermediate water levels, optimal temperature, and light penetration, as well as slow winds were the prevailing conditions in Laguna de Rocha. SW winds, which are the most important in this lagoon, are less frequent during summer on the Uruguayan coast (Panario & Piñeiro, 1997).

During the isolation period prior to the March 2003 sampling, SAV freshwater species from the fluvial system, as well as low salinity tolerant species could have colonized. Under this condition, SAV richness and biomass could have increased. This hypothesis is sustained by the following evidence: (1) the colonization of *P. pusillus* (a typical freshwater species, Schütz Rodrigues & Irgang, 2001) in zone B in March 2003, and in one sampling point in zone A close to the outlet of Rocha stream also in March 2003 and December 2003. *Egeria densa* Planch. was found during summer 2001 at the outlet of Rocha stream close to B and A sampling sites (pers. obs.), but never developed stable populations, probably due to its low tolerance to salinity (Haunstein & Ramirez, 1986); (2) Tubers of *P. pectinatus* were found all over the northern area during the study period (data not shown), indicating no limitation of propagules for colonization; and (3) light penetration reached the sediments most of the time and nutrient concentrations in the sediments were well above limiting levels (Barko et al., 1986 and references therein); also, sediment particle size in the lagoon is fine sand to coarse silt (Sommaruga & Conde, 1990), which is within the tolerance range for most of the species (Kantrud, 1990, 1991). Therefore, no other limiting factor may have limited SAV growth during the isolation period prior to our first sampling.

Once the sand bar was opened and the marine intrusion reached the North, less tolerant species disappeared, decreasing SAV biomass and richness. Even *R. maritima* and *Z. palustris* could have been affected in the northern areas by a rapid change in conductivity, explaining its lower biomass after March 2003. Conductivity was 0.7 mS cm^{-1} in zone A and 14.1 mS cm^{-1} in zone C during March 2003 sampling, indicating a marine intrusion progressing toward the North. In contrast, SAV biomass was stable in southern stations during the study period, probably due to more stable brackish conditions.

SAV effects on water quality

Despite the ephemeral dominance by SAV in northern areas in March 2003, important effects on water characteristics were observed. During SAV proliferation, suspended solids and total nutrients were affected, suspended solids were five times lower inside SAV patches while total phosphorus and total nitrogen were three and two times lower, respectively. During the aerial survey, it was evident that patches of SAV produced quiet water while in open waters turbulent surfaces were observed due to coastal winds. At high biomass values (200 g DW m^{-2}) submerged species such as *M. sibiricum* and *Chara* spp. can prevent sediment resuspension even at high wind speeds ($>30 \text{ km h}^{-1}$), whereas at lower biomass (20 g DW m^{-2}) they can substantially reduce resuspension near the sediment surface (James et al., 2004). In addition, SAV can lower background SS by promoting deposition (James & Barko, 1990). James et al. (2004) attribute the lack of resuspension in a shallow lake to the occurrence of high SAV biomass in contrast to following years with lower SAV biomass. It seems that SAV ephemeral proliferation in Laguna de Rocha acts as an effective suspended solids and total nutrients trap, because biomass was within the range reported by James et al. (2004). This can have important long-term ecosystem implications in scenarios of climate and land use changes.

SAV ephemeral proliferation could also be a partial response of the system to other processes like eutrophication, which seems to be accelerating in Laguna de Rocha (Aubriot et al., 2005) due to intensification of land use in the basin (Rodríguez-Gallego et al., 2009). Under these assumptions, it could be hypothesized that more nutrients are exported from the catchment to the

lagoon and that during periods of isolation from the ocean the lagoon can develop rapid internal mechanisms—plant driven—to attenuate eutrophication impacts on water quality. This underlying mechanism includes nutrient control due to resuspension reduction, suspended solids trapping inside SAV patches and enhanced denitrification at the water–plant–sediment interface (Weisner et al., 1994). This hypothesis is also based on the climate change predictions for Uruguay, which state increased precipitation and runoff affecting mainly the coastal zone (Genta et al., 1998). Therefore, increase in the frequency and duration of this SAV ephemeral phenomenon might be expected and it could become more frequent in other coastal lagoons of the region.

Structuring role of SAV on zoobenthos

The zoobenthic species composition and distribution in Laguna de Rocha were similar to reports by other authors (Pintos et al., 1991; Arocena, 2007). Two different assemblages were identified: (1) a typically estuarine assemblage with taxa distributed in the whole system or exclusively in the southern area; this assemblage was similar to Pintos et al. (1991) findings; and (2) a SAV-associated assemblage which was dominated by insects, mostly chironomid larvae. This assemblage was found mainly in the zone B during the SAV proliferation in March 2003 and was similar to the results reported by Arocena (2007) in the same bay. The typical estuarine benthos assemblage was more abundant than the SAV-associated one.

In contrast to our results, Pintos et al. (1991), Arocena (2007), and Rodríguez-Graña et al. (2008) found *Heleobia* spp. and *E. mactroides* in northern and southern areas, but generally with higher abundance in the South. Probably lower conductivity during the isolation period could have affected the distribution of these estuarine species in the northern area. Insect larvae, including chironomids, were present in northern SAV stands and some were also present in northern unvegetated zones, but were always absent in the South. Most of them disappeared after the March 2003 SAV proliferation. Similar results were found by Arocena (2007). Chironomids often form a major proportion of the macroinvertebrate fauna of different aquatic plants (Learner et al., 1989).

The zoobenthic community was strongly affected by SAV but only at northern stations, mainly during

SAV proliferation in March 2003. These results indicate that SAV could be a very important structuring factor for zoobenthos in coastal lagoons. SAV could become an important habitat for the typical estuarine species and also promote colonization by new zoobenthos species, increasing richness and also abundance. However, the lack of differences in zoobenthos structure between SAV and unvegetated areas in the South as well as in A and C zones after the SAV proliferation in March 2003, could indicate the existence of a threshold of SAV biomass above which effects on the zoobenthos might be observed. A threshold of 100 g DW m^{-2} seems to be sufficient, since that is the stable biomass observed in the zone B, where the major structuring effects were observed. This could explain North–South differences, since SAV was an order of magnitude lower in the South and in A and C zones after March 2003.

Furthermore, the more stable brackish conditions in the South could determine a more abundant typically estuarine assemblage of zoobenthos, but with lower richness. Levin and Talley (1999) hypothesize that in physically dominated environments, vascular plants can enhance macrofaunal communities by reducing stress. A larger conductivity fluctuation in northern zones could imply a more variable zoobenthos assemblage and also a higher structuring effect of SAV above certain biomass thresholds.

The variance partitioning analysis confirmed the important structuring role of SAV proliferation on zoobenthos. SAV explained most of the total variance of zoobenthos abundance in Laguna de Rocha, while hydrological related variables explained a lower but also an important proportion. An outstanding result is that the shared variance was high, probably because both SAV and zoobenthos depend on the similar hydrological-related variables.

Potential effects on the food web

A recent reconstruction of the food-web of the Laguna de Rocha with stable isotopes (Rodríguez-Graña et al., 2008) showed a strong dependency of most components on the benthic compartment, and zoobenthos seems to be one of the key features of the trophic structure. Although macrophytes were not directly used as food sources, the scaling effects on the trophic web should not be underrated due to the structuring effects on the zoobenthos community. Also, their

trophic importance could be underestimated since aquatic birds were not incorporated into the model. Herbivorous birds such as black necked swans (*Cygnus melanocoryphus*) are very abundant in this lagoon (Vaz-Ferreira & Rilla, 1991) as well as coscoroba swans (*Coscoroba coscoroba*) and coots. This hypothesis is supported by the fact that these species are generally observed feeding in the system (Sarroca, 2008) and that specimens of *P. pectinatus* with indications of herbivory were observed during March 2003. Also, preliminary stomach content analysis of dead swans of Laguna de Rocha showed important biomass of *R. maritima* and *Z. palustris* (Rodríguez-Gallego, pers. obs.). Therefore, SAV could be a key issue for conservation efforts in the Laguna de Rocha protected area as well as in other similar coastal lagoons in the region, indicating the need for specific management recommendations. For example, fisheries and bird-watching by boat should be avoided in vegetated zones, to prevent SAV dislodgement.

SAV as a physical heterogeneity driver

Conde et al. (2000) stated that the salinity gradient is the main spatial heterogeneity promoter in Laguna de Rocha, driven by the sand bar opening and marine intrusions. They described three hydrological states: (1) the lagoon is completely limnic before the sand bar opens; (2) the lagoon is completely brackish if the marine intrusion is pushed toward the North by coastal winds; (3) the lagoon is brackish in the South and has limnic in the North as an intermediate situation. Bonilla et al. (2005) found that hydrology determines the phytoplankton community which is more important than seasonality. Also, Piccini et al. (2006) found that hydrology determines bacteria abundance and production. Our results showed that although hydrology is the strongest structuring factor in Laguna de Rocha for water chemistry, plants and other communities, SAV can also be an additional structuring local factor when biomass exceeds a certain threshold (i.e., 100 g DW m⁻²). Zoobenthos richness and abundance increased in vegetated zones while suspended solids and total nutrients decreased due to enhanced sedimentation. Therefore, SAV biomass could be the main structuring factor for benthos and also contribute to reduce resuspension, which could be also expected in other shallow coastal lagoons where SAV proliferations could develop.

Conclusions

SAV ephemeral proliferations in Laguna de Rocha could be a response of the system to long-term changes of eutrophication and increased precipitation due to climate change. When long isolation periods of the lagoon from the ocean coincides with freshwater conditions and the summer season, less salinity tolerant macrophytes can colonize the northern zones of the lagoon, increasing SAV biomass, cover, and richness. However, when the sand bar is opened the marine intrusion can progress to northern zones and the salinity increase could promote SAV biomass and richness decrease. When these ephemeral proliferations of SAV occur, several changes in the physico-chemical characteristics and biological communities can be observed. SAV decreases water turbulence and reduces sediment resuspension, promoting the reduction of total nutrients of the water. Furthermore SAV can also increase the spatial heterogeneity and offer habitat for zoobenthos species, promoting the increase of benthos richness and abundance. This in turn could increase the productivity of the whole system since zoobenthos appears as the main energy pathway in the trophic structure of this system. SAV proliferations could become frequent in other coastal lagoons of the region, which could promote changes in their functioning. Therefore, SAV ephemeral proliferations could be an early warning of long-term changes in the coastal zone.

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Anexo II - Establishing limits to aquaculture in a protected coastal lagoon: impact of *Farfantepenaeus paulensis* culture pens on water quality and benthic biota

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Establishing limits to aquaculture in a protected coastal lagoon: Impact of *Farfantepenaeus paulensis* pens on water quality, sediment and benthic biota

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Abstract

Aquaculture is perceived by governments and international agencies as an economic alternative for poor communities in developing countries. Nevertheless, aquaculture must address environmental issues as well as economic and social aspects to achieve a sustainable development. Aquaculture with native species under semi-intensive conditions is a sustainable production alternative that minimizes the impact on aquatic ecosystems. An aquaculture pilot project with pink shrimp (*Farfantepenaeus paulensis*) was tested in a protected lagoon in Uruguay (Laguna de Rocha). Shrimp were reared in pen enclosures within their native habitat, where natural currents drive water renewal, and the natural food supply was supplemented with commercial food. The aim of this study was to evaluate the impact of *F. paulensis* aquaculture on the water and sediment quality and the benthic community, and to estimate the maximum number of pen enclosures that Laguna de Rocha can sustain while maintaining the minimal environmental impact. A Before, After, Control Impact (BACI) sampling design was followed and the results of abiotic and biological variables were compared between treatment site (control, pens, and two areas at 15 and 50 m from the pens) and timing (before shrimp addition, during culture and after harvest), through ANOVA. The most significant impact was found inside the pens, where ammonium levels increased and benthos species richness and abundance decreased. A nitrogen-based-model was used to estimate the maximum number of pens in relation to the minimal impact on the ecosystem. Simulation indicated that up to 13 pens could be installed in the southern area of Laguna de Rocha without increasing the usual concentration of total nitrogen in other areas of the lagoon. The BACI design, the statistical analysis and the modeling tools proved to be effective, simple and low cost instruments to assess the environmental impact in a protected area.

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Keywords: Environmental impact assessment; Pink shrimp; Sustainable aquaculture

1. Introduction

Presently, management efforts in protected areas admit the feasible coexistence of economic activities and the conservation of biodiversity (Brockington et al., 2006; Wilkie et al., 2006). Native shrimp aquaculture under semi-intensive conditions (i.e.

pen enclosures or culture pens) could represent a sustainable production alternative that improves the welfare of human communities in conservation areas, minimizing the environmental impact of more intensive systems and avoiding the introduction of potentially invasive species. In pen enclosures, shrimp are reared in their indigenous habitat, shallow estuaries or brackish lagoons, where natural currents drive water renewal. The natural food supply, e.g. fisheries leftovers and benthic organisms naturally occurring inside the enclosures, is balanced with commercial food, particularly during early stages of development (Soares et al., 2004; Wasielesky et al., 2004).

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Pen enclosures circumvent several negative aspects of aquaculture (Wasielesky et al., 2004). Due to low implementation costs, fishermen own this family based production system, therefore avoiding their dependence on private intermediaries (González et al., 2003). Production in pen enclosures also contributes to the stabilization of shrimp production in comparison with the natural variability of landings, which depend on the post-larvae entrance into the estuaries during the marine intrusion (Reis and D'Incao, 2000). While this technique does not significantly modify the natural habitat nor compete with other fisheries because little area is required, the amplified areal grazing by shrimp on the benthic community is its major drawback (Nunes and Parsons, 2000; Soares et al., 2004). Nevertheless, this type of aquaculture has been successfully implemented with pink shrimp (*Farfantepenaeus paulensis*) in Lagoa dos Patos in southern Brazil and exhibited only minor environmental impact (Soares et al., 2004).

Following the experience in Lagoa dos Patos, a similar pilot initiative was implemented in Laguna de Rocha (Uruguay), a natural brackish coastal lagoon inside a National Park and Biosphere Reserve. This lagoon maintains one of the most traditional artisanal inland fisheries of Uruguay, sustaining more than 20 families. Decision makers and the local community perceive the pink shrimp initiative as an economical solution to cope with poverty, while for conservationists it represents a threat to the natural functioning of the lagoon. The commencement of this initiative in 2004 reestablished the discussion on how to limit emergent economic development in this protected coastal area. Should economic activities or biodiversity conservation be prioritized? Is there any possible in-between alternative?

Environmental impact studies (EISs) have been proposed as valuable tools to foster public scrutiny of economical activities in natural areas, allowing the evaluation of techniques and environmental alternatives (Bojórquez-Tapia et al., 1998). However, while the assessment could be designed to maximize the power of impact detection, EISs have methodological restrictions (Osenberg et al., 1996). The BACI design (Before, After, Control, Impact), on the other hand, reduces the degree of uncertainty of EISs, permitting the comparison of impacted and non-impacted sites. BACI seeks for an interaction between the effects of sites and time, since differences detected before and after the impact can provide an estimate of their magnitude (Osenberg and Schmitt, 1996). In addition, potential impacts not detected due to sampling limitations can be quantified, which is essential given the uncertainty resulting from the complexity of natural systems and the need to increase precaution in the decision making process (Mapstone, 1996; Osenberg et al., 1996).

Numerical modeling is another tool commonly used in the decision making process for coastal issues. For example, it allows the generation of different scenarios, the evaluation of the effectiveness of pollution control and the determination of the carrying capacity of specific water bodies, as well as the prediction of environmental impacts in coastal and estuarine ecosystems. Regarding aquaculture, several models of diverse complexity allow the prediction of the environmental impacts of specific cultures (Twilley et al., 1998; Dudley et al., 2000;

Handerson et al., 2001; Daglioli et al., 2004). However, even utilizing complex models, there are certain limitations to the prediction because most of the models were developed for different environments or for different species.

The aim of this study was to evaluate the impact of *F. paulensis* pen aquaculture on the benthic community and on the water and sediment quality in Laguna de Rocha Lacustrine National Park (Uruguay), as well as to estimate the maximum number of pens that the lagoon can sustain with minimal environmental impact.

2. Methodology

2.1. Study area

Laguna de Rocha (Rocha, Uruguay; 34° 35' S–54° 17' W) (Fig. 1) is a nursery and reproductive area for important regional fish resources (Fabiano et al., 1998; Vizziano et al., 2002; Norbis and Galli, 2004) and for resident and migratory aquatic birds (Morrison et al., 1989; Rilla, 1992, 1993). The lagoon is included in the MaB-UNESCO Reserve “Baños del Este” and is presently being inducted into the National System of Natural Protected Areas.

The lagoon (surface area 72 km²; average depth 0.6 m) connects periodically with the Atlantic Ocean through a channel that opens in the sandbar (Conde et al., 1999). The periodic interaction of water masses of limnic and marine origins is the driving force for the functioning of the whole ecosystem (Conde et al., 2000, 2002; Bonilla et al., 2005; Giménez et al., 2005). Fisheries of brackish and marine species depend on these hydrological dynamics because the entrance of fish and crustacean larvae and the spawning of adults are tightly coupled to the marine intrusion (Vizziano et al., 2002). In this system, the average concentration of dissolved inorganic nitrogen and reactive soluble phosphorus for the last decade was 27.3±29.2 and 133.2±315.4 µg l⁻¹, respectively, while their atomic relation was 13.4±28.4 (Bonilla et al., 2006).

Land use in the watershed has been committed predominantly to extensive cattle raising, but a substantial increase in agricultural area has occurred during the last decade (L. Rodríguez-Gallego, unpub.). The lagoon is influenced by several activities in the nearby beach resort, La Paloma, and receives, through its main tributary, the primary-treated wastewaters of Rocha City (30,000 inhabitants). There is evidence that the lagoon is experiencing a eutrophication process. For example, an increase of total phosphorus and chlorophyll, high epiphytic microalgal biomass (Conde et al., 1999), recent episodes of potentially toxic cyanobacteria (*Pseudoanabaena* sp. and *Microcystis*) (V. Hein, pers. comm.) and proliferation of submerged hydrophytes have all been noted. The natural hydrology is also modified (i.e. the artificial opening of the sand bar to avoid flooding and to allow entrance of commercial larvae). The above creates challenges to the environmental well-being of the lagoon.

Two artisanal fishing communities have developed a family based artisanal fishery based on *Paralichthys orbignyanus*, *Odontheistes argentiniensis*, *Micropogonias furnieri*, *Brevoortia aurea* among fishes, and *Callinectes sapidus* and *F. paulensis* among crustaceans (Santana and Fabiano, 1999). Annual income per family is less than US\$ 250. Pink shrimp trapping starts at the end of summer (March) and continues until mid autumn (May), and captures are highly variable between consecutive years. Littoral currents from the waters of Southern Brazil drive larvae to this coastal area, entering the lagoon in late spring (October–December) (Santana and Fabiano, 1992).

2.2. Experimental procedure and monitoring

2.2.1. Pink shrimp aquaculture in pen enclosures

In 2003 and 2004, the fishing community located in the Southern area of Laguna de Rocha (Fig. 1) carried out a pilot aquaculture experience. Pink shrimp larvae were produced at the Mariculture Laboratory of FURG and the post-larvae were transported in plastic bags at 19 °C under oxygenation to Laguna de Rocha. After acclimatization to water temperature, they were inoculated into nursery pens of 15 m in diameter and 2 m height, with a mesh of 0.1 mm pore size. Four pen enclosures were set up at ca. 100 m from the shore (depth range

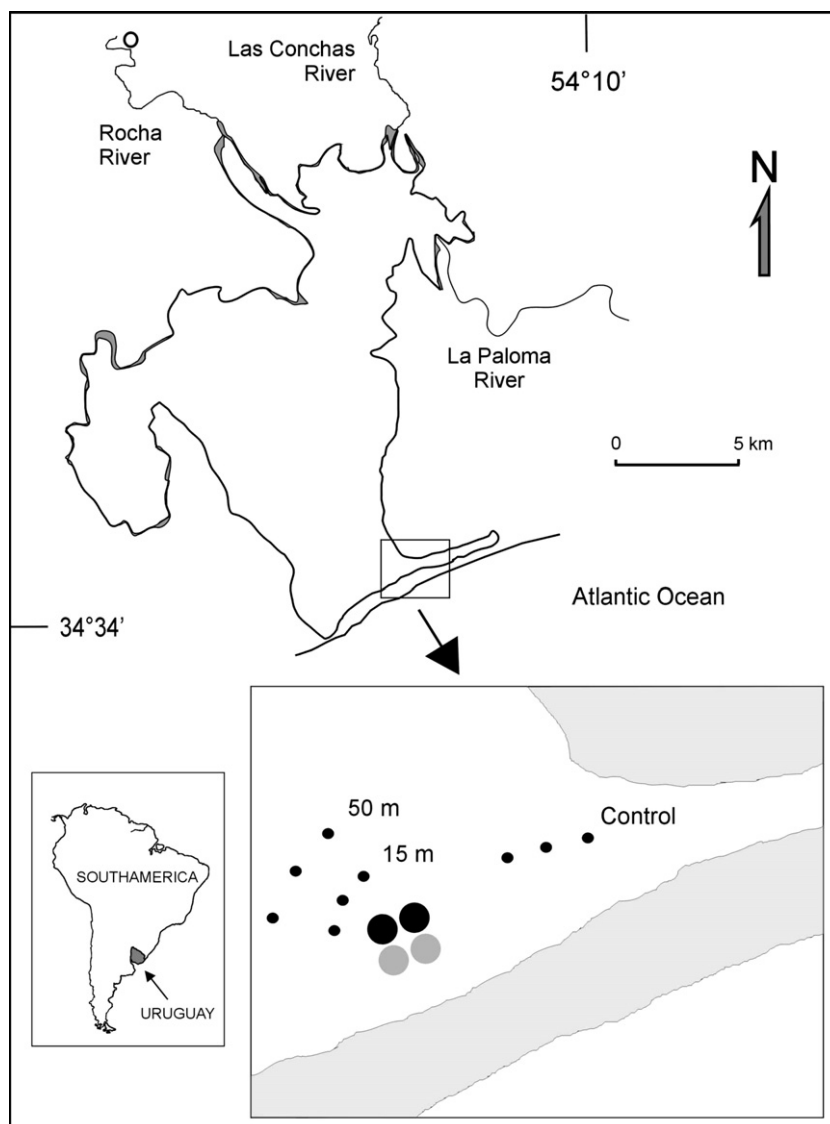


Fig. 1. Map of Laguna de Rocha, showing the study area at the southern end of the system. The sketch indicates the location of the pen enclosures (big circles; the black ones were the two pens sampled for this study), and control, 15 and 50 m sites where the impact was evaluated (small black circles show the location of replicates).

from 50 to 100 cm). Two enclosures contained a post-larval density of 20 shrimp m^{-2} and two contained 30 shrimp m^{-2} . During 35 days, shrimp were maintained inside inner nurseries, until 99% of the shrimp reached a weight of 0.35 g. Subsequently, nurseries were lifted, keeping the shrimp in a growth outer pen of 30 m in diameter with a mesh size of 5 mm until harvesting. Food, supplied four times a day, was composed of fish and crab from fishery by-catch, and pelleted shrimp food. The weight of the shrimp was determined every two weeks, allowing for adjustments to the feeding rate.

Shrimp harvest started at the end of April. However, the harvest was finished at the beginning of May due to an increase in the lagoon water level after rainfall events in the watershed. According to estimates, one third of the population was inside the pens at the moment of the last sampling.

2.2.2. Sampling design

Sampling was conducted based on the BACI design (Osenberg and Schmitt, 1996), but with minor modifications. The affected area consisted of the two pen enclosures with higher post-larval density. The control site was an area with similar physical and biological features to those of the affected area and according to the predominant water movement towards SW, was not influenced by the enclosures. Two areas located at 15 and 50 m from the pens were sampled

to evaluate the gradient of the potential impact (Fig. 1). All sites were sampled before inoculation (December 2003), during culture (April 2004) and after harvest (June 2004) for all abiotic and biological parameters. At each area, three replicates of all variables were taken at random, with the exception of the samples taken inside the pens (one replicate in one pen and two replicates in the second one). The two pens with lower larval density were not sampled, under the assumption that the impact in those enclosures would be equal or less than in those pens with higher density. Due to the incomplete harvest, the recovery of the system after pens removal could not be evaluated.

For each sample, abiotic parameters were determined *in situ* using field equipment: depth (manual sound), pH and conductivity (K; Horiba D-24), photosynthetically active radiation (PAR) to derive PAR attenuation coefficient (K_d PAR; 400–700 nm) (LI-COR LI 250), temperature and dissolved oxygen (T and DO; Horiba D-25). After verifying the complete mixing of the water column through DO and T profiles, water samples were taken under the surface with a Ruttner bottle, to be later analyzed for total and organic suspended solids (SS and OM, respectively; APHA, 1985), ammonium (NH_4 ; Koroleff, 1970), nitrite (NO_2 ; Strickland and Parsons, 1972), nitrate (NO_3 ; Mackereth et al., 1978), total nitrogen (TN; Mackereth et al., 1978), soluble reactive phosphorus (SRP; Murphy and Riley, 1962) and total phosphorus (TP; Valderrama, 1981).

Table 1
Average concentration and range of all abiotic variables in water and sediments of Laguna de Rocha during the study period

Variable	Average	Range	
Z (m)	0.8	1.2	0.4
T (°C)	16.3	10.4	20.4
DO (mg l ⁻¹)	10.9	8.2	14.1
pH	8.1	8.4	8.5
K (mS cm ⁻¹)	15.2	7.4	22.1
K _d PAR (m ⁻¹)	1.9	1.0	3.6
SRP (μg l ⁻¹)	36.5	nd	525.2
TP (μg l ⁻¹)	81.3	38.1	618.3
NH ₄ (μg l ⁻¹)	21.2	nd	124.9
NO ₂ (μg l ⁻¹)	0.9	nd	1.9
NO ₃ (μg l ⁻¹)	7.2	nd	15.4
TN (μg l ⁻¹)	795.4	467.9	1157.5
SS (μg l ⁻¹)	30.2	13.8	58.2
OM (μg l ⁻¹)	8.4	1.9	15.0
OMsed (%)	2.3	0.6	10.5
TPsed (μg g ⁻¹ dw)	132.0	48.0	365.0
TNsed (μg g ⁻¹ dw)	105.4	nd	342.1

nd: not detectable. See abbreviations in the text.

Sediment samples were manually collected down to a depth of 2 cm using a 5 cm diameter acrylic corer. The organic content of the sediment was determined by ignition (OMsed; APHA, 1985) and TN (TNsed) and TP (TPsed) according to Valderrama (1981). Benthos samples were collected similarly down to a depth of 10 cm. Five samples were collected and grouped at each sampling area for analysis. Samples were transported in plastic bags to the laboratory and sieved

through a 0.5 mm diameter mesh. Organisms were preserved in alcohol (70%), identified at the species level and quantified.

2.2.3. Environmental sustainability of the activity

To determine the environmentally optimum number of pens, we used a nitrogen-based model originally developed for low circulation embayments in Lagoa dos Patos (Poersch, 2006), which has similar abiotic characteristics to those observed at Laguna de Rocha. The theoretical estimation of nitrogen input caused by the enclosures was performed based on Poersch (2006), assuming that:

- 1) the protein contains 16% nitrogen (Holland et al., 1991), i.e. 1 kg of shrimp has 178.5 g of protein and 28.56 g of nitrogen (Boyd and Teichert-Coddington, 1995);
- 2) the feed (Purina®) contains 30% protein;
- 3) the feeding rate (FR) is described as: $FR = 0.56 \times (\text{individual weight})^{-0.5}$;
- 4) the quantity of feed (QF) needed for a pen is calculated as: $QF = FR \times \text{the biomass in the pen}$;
- 5) 15% of the given feed is not consumed (NC) (Primavera, 1993);
- 6) food ingestion (IN) is calculated as: $IN = QF - NC$;
- 7) of the total amount ingested, some is digested (DI) and some is not. The digested food is transformed into growth (GR) and excretion (EX), and the undigested into faeces (FC). Thus: $FC = 100 - DI$ and $EX = IN - (FC + GR)$;
- 8) 30% of the food ingested is transformed into growth (GR) (Montoya et al., 1999);
- 9) 90% of the protein in the food is digestible (Montoya et al., 1999);
- 10) a mortality rate of 20% at the end of the rearing process is acceptable;
- 11) the initial weight of the shrimp is 0.35 g (Wasielensky, 2000);
- 12) the initial number of shrimp per pen (0.3 ind. m⁻² ha⁻¹) was 60,000 (20 ind. m⁻²).

Table 2
Two-way ANOVA for time, treatments and time-treatment interaction for water, sediment and biological variables in Laguna de Rocha

Variable	Time	Treatment	Interaction
<i>Water</i>			
T	ns	ns	ns
DO	ns	ns	ns
pH	ns	ns	ns
K	ns	ns	ns
K _d PAR	ns	ns	ns
SRP	Mann Whitney tests are not shown	ns	ns
TP	Mann Whitney tests are not shown	ns	ns
NH ₄	$F_{(2,2)} = 7.940, p < 0.05$	$F_{(2,3)} = 7.620, p < 0.001$	$F_{(2,6)} = 3.445, p < 0.05$
NO ₂	$F_{(2,2)} = 57.8, p < 0.001$	$F_{(2,3)} = 3.5, p < 0.05$	
NO ₃	$F_{(2,2)} = 23.8, p < 0.001$	ns	ns
TN	ns	ns	ns
SS	$F_{(2,2)} = 14.038, p < 0.001$	$F_{(2,3)} = 4.059, p < 0.05$	ns
OM	$F_{(2,2)} = 12.713, p < 0.001$	ns	$F_{(2,6)} = 4.513, p < 0.005$
<i>Sediment</i>			
OMsed	$F_{(2,2)} = 26.169, p < 0.001$	$F_{(2,3)} = 3.896, p < 0.05$	ns
TPsed	$F_{(2,2)} = 7.803, p < 0.005$	ns	ns
TNsed	$F_{(2,2)} = 9.641, p < 0.001$	ns	ns
<i>Benthos</i>			
Richness	$F_{(2,2)} = 5.148, p < 0.05$	$F_{(2,3)} = 6.716, p < 0.01$	$F_{(2,6)} = 3.123, p < 0.05$
Total abundance	ns	$F_{(2,3)} = 16.999, p < 0.001$	$F_{(2,6)} = 6.051, p < 0.005$
<i>Heleobia</i> sp.	ns	$F_{(2,3)} = 14.568, p < 0.001$	$F_{(2,6)} = 4.797, p < 0.001$
<i>E. mactroides</i>	ns	$F_{(2,3)} = 3.212, p < 0.01$	$F_{(2,6)} = 4.311, p < 0.01$
<i>N. fluviatilis</i>	$F_{(2,2)} = 90.7, p < 0.001$	ns	ns
<i>H. similis</i>	$F_{(2,2)} = 25.3, p < 0.001$	ns	ns
<i>D. fluminensis</i>	$F_{(2,2)} = 28.2, p < 0.001$	ns	$F_{(2,6)} = 4.3, p < 0.05$

ns: non-significant. See abbreviations in the text.

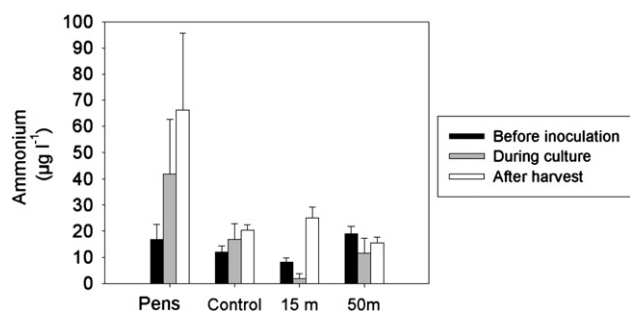


Fig. 2. Ammonium concentration in all treatments in Laguna de Rocha during the study. The standard error is indicated ($n=3$).

After determining the nitrogen contribution of each enclosure, the second phase of the model estimates the maximum number of pen enclosures that the lagoon can sustain while maintaining the minimal environmental impact. A conservative approach was followed assuming that: 1) the pen's mesh affects the natural water circulation by ca. 15%; 2) the speed of the water current is always more than 0.001 m s^{-1} ; 3) the natural concentration of nitrogen in the lagoon is $760 \text{ } \mu\text{g l}^{-1}$ (i.e. the mean TN concentration at the control site during the study, and a representative value of normal conditions) (Bonilla et al., 2006); 4) the uptake and mineralization of nutrients and organic matter by microorganisms is negligible; 5) all the nitrogen accumulated in the sediment during the rearing process is released to the environment during harvesting.

2.2.4. Data analysis

Parametric analyses of variance (Two-way ANOVA with fixed effects) were performed according to Zar (1999). The homoscedasticity of the variance was proven with the Bartlett and Cochran test and the normality with the Kolmogorov Smirnov test. A logarithmic transformation was used for benthos richness and abundance, NH_4 and OMsed. SRP and TP concentrations did not fulfill the normality assumptions even after testing different transformations. They were therefore compared, considering the variables of timing and type of treatment by using the non-parametric Mann–Whitney test (Zar, 1999). For the main variables, 95% confidence intervals ($\text{CI}_{95\%}$) were calculated. The statistical power of the ANOVA was estimated for the treatment factor and the interaction among treatments and time only when significant differences were not detected. This allowed for the determination of the probability of not detecting an impact on the variable analyzed given that a real effect existed (β type error). To compute the statistical power, large (0.40) and medium (0.25) effect sizes were used (Cohen, 1988).

3. Results and discussion

3.1. Impact on water and sediment variables

Table 1 presents the average concentration and range of abiotic variables of water and sediments for the study period. The results of the statistical analysis performed using water, sediment and benthos variables are shown in Table 2. Water depth showed an oscillation in a normal range, diminishing towards the post-harvest sampling period. Water T showed a decrease from spring to fall, while the contrary was observed for DO, being always close to saturation. pH values were fairly constant, and PAR reached the surface sediments in all sampling occasions. K values showed brackish conditions throughout the whole study period, the variability being determined by marine intrusions. No differences between surface and bottom water were observed for any of the *in situ* parameters, indicating that the water column was always mixed. None of these parameters showed differences between treatments or interactions between factors. Values observed for all *in situ* parameters were within the normal range for the system (Bonilla et al., 2006).

The concentration of NH_4 revealed significant differences over time, between treatments and for the interaction between factors. The values were higher inside the pens with shrimp after the harvest (Fig. 2), but in

all cases remained below potentially toxic levels for fishes (0.5 mg l^{-1} ; Roldán Pérez, 1992). Concentrations of SRP and TP did not show significant differences between treatments, being higher during culture in both cases. NO_2 and NO_3 were higher before the shrimp larvae addition to the pens and lower in April, during the culture. NO_2 levels also revealed differences between treatments, reaching maximum values at a distance of 15 m from the pens. TN values did not present differences in between time nor treatments. Concentration of SS was higher after the harvest and lower in the control area. Solely OM demonstrated differences in treatment timing, being lower during the culture, and presented interaction between factors.

OMsed was higher after the shrimp harvest in all samples, but lower inside the pens than in the control area and never exceeding 10% of the dry weight of the sediment. OMsed did not show interaction between factors. TNsed was lower before the addition of shrimp larvae and was maximum after the harvest, without differences between treatments and without interaction between factors. TPsed was higher after the harvest, without differences between treatments or interaction. In all the cases, the values of the variables were in the natural range registered by different studies performed in the Southern area of Laguna de Rocha (Conde et al., 2002; Bonilla et al., 2005; Bonilla et al., 2006).

The significant differences observed between samplings, the absence of major differences between treatments for most of the chemical variables and the scarce interaction between factors (only two variables showed interaction) suggest that the natural circulation of the water is the major factor in determining the concentration of nutrients and organic material in the water and sediment. A similar phenomenon was registered in Lagoa dos Patos (Soares et al., 2004). However, NH_4 concentration was higher in the pens, increasing considerably with the addition of the shrimp larvae. This could be explained by the shrimp excretion (Schmitt and Santos, 1998), as well as that of crabs (*Chasmagnathus granulatus*) which invaded the pens following the

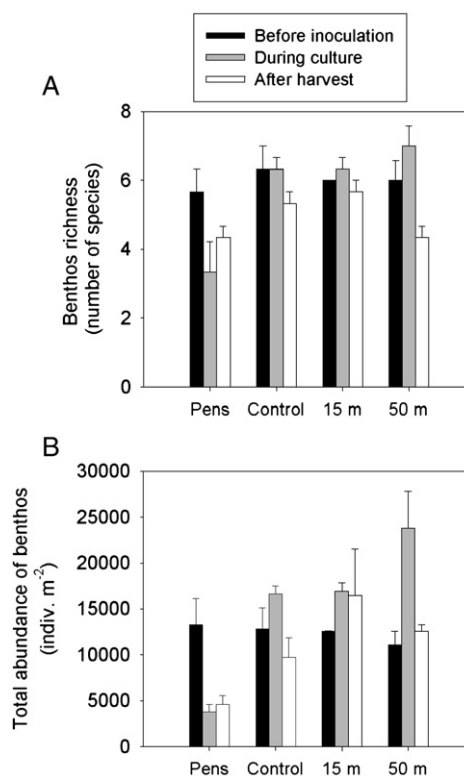


Fig. 3. Species richness (A) and total abundance (B) of the benthic community in different treatments in Laguna de Rocha. The standard error is indicated ($n=3$).

Table 3
Average density of the most abundant benthic organisms in all samplings in Laguna de Rocha

Species	Before inoculation		During culture		After harvest	
	Pens (ind. m ⁻²)	C,15,50 (ind. m ⁻²)	Pens (ind. m ⁻²)	C,15,50 (ind. m ⁻²)	Pens (ind. m ⁻²)	C,15,50 (ind. m ⁻²)
<i>Heleobia</i> sp.	6662±1811	6223±1008	2650±517	33980±5791	2945±657	23454±6295
<i>N. fluviatilis</i>	972±51	1011±155	0	593±133	294±106	452±144
<i>H. similis</i>	913±235	844±223	59±29	1014±228	206±77	608±194
<i>D. fluminensis</i>	1209±29	677±213	59±29	998±332	88±0	421±214
<i>E. mactroides</i>	117±29	108±34	118±77	530±160	0	468±151

The results from the control, 15 m and 50 m sites were grouped (C,15,50). The standard error is indicated. $n=3$ for the pens and $n=9$ for the grouped treatments.

high food offering. High concentration of NH₄ could be also due to the mineralization of commercial pelleted food, which can account for up to 78 and 51% of the N and P input, respectively, to cultivated ponds (Funge-Smith and Briggs, 1998).

Conversely, OMsed decreased inside the pens, possibly due to the detritivorous and benthivorous feeding habits of shrimp (Dall, 1968). However, no interaction was detected, indicating that the decrease could be ascribed to other reasons rather than cultivation. Contrasting results have been detected in the region. While Esteves et al. (1999) reported an OMsed decrease in pen cultures, Soares et al. (2004) did not find differences. Nevertheless, it would be important to evaluate whether or not the nutrients accumulated in the sediment (mainly phosphorus entering the system through the shrimp food) are associated to iron complexes. This association increases the phosphorus internal load (Jensen et al., 1992), therefore generating a potential long term impact through eutrophication.

The power of the statistical analysis for a large effect size (0.4) was always higher than 0.7 for the interaction between treatments and higher than 0.95 for the time and treatment factors. This indicates that the probability of falsely rejecting the hypothesis of no impact is too low. For a medium effect size (0.25), the power decreases, taking values of 0.3 for the interaction and 0.55 for the treatments, but maintaining acceptable probabilities of committing a β type error.

3.2. Impact on the benthic community

The benthos was composed by the gastropod *Heleobia* sp., the polychaetes *Nephtys fluviatilis* and *Heteromastus similis*, the bivalves *Erodona mactroides* and *Tagehus plebeius*, the crustaceans *Cassidini-dea fluminensis*, *Cyrtograpsus angulatus* and *Sinelobus stanfordi* and a

non-identified amphipod. The benthic species richness was significantly lower inside the pens with shrimp (Fig. 3A), decreasing from an average of six species in the sampling before shrimp inoculation (CI_{95%} 6±0.5) to four species inside the pens (CI_{95%} 4±1.2) and to six species in the remaining treatments after the harvest (CI_{95%} 6±0.5). Both factors demonstrated interaction. The total abundance of benthic invertebrates was significantly lower inside the pens (CI_{95%} 7181±3371), with a 49% reduction in comparison to the control treatments (Fig. 3B) (CI_{95%} 14725±2149). There was no difference in abundance over time, but interactions between factors were exhibited (Table 2).

The abundance of *Heleobia* sp. and *E. mactroides* was lower inside the pens during culture. The abundance of *Heleobia* sp. and *D. fluminensis* demonstrated interaction between factors (Table 2). *D. fluminensis*, *H. similis* and *N. fluviatilis* abundances were higher during the sampling before shrimp addition but did not show differences between treatments (Table 3).

Conversely to what was observed for the abiotic variables, the impact of the shrimp cultivation on the benthos was obvious. This was seen in the decreased species richness and total abundance of organisms inside the pens and was also related to an interaction between time and treatment factors. The interaction indicates a non-equal behavior in time between treatments with and without shrimp, attributable to the cultivation. However, this impact presents a localized occurrence restricted to the pens, and no effects were evident in the treatments at 15 and 50 m from the pens.

The impact on the benthic community inside the pens can be explained by direct predation of shrimp on these organisms, and also by the sediment disturbance caused by their burial activity. Although some authors classify Penaeid shrimp as detritivorous (Dall, 1968), it has been demonstrated that their diet is diverse. Diversified diets

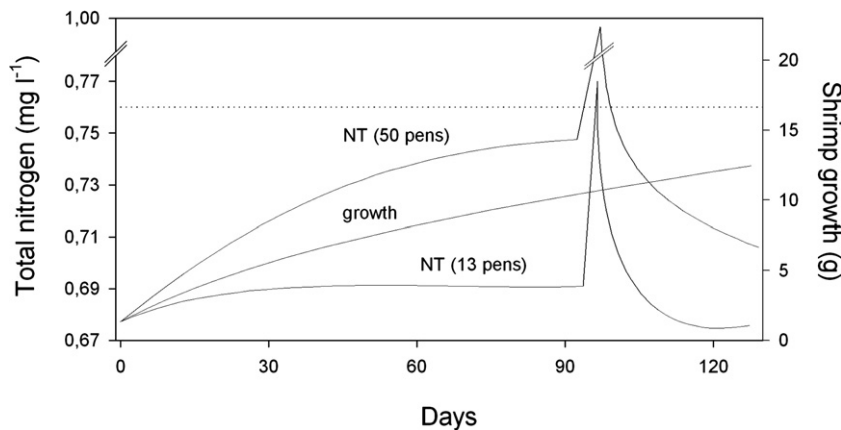


Fig. 4. Simulation of the effects of 13 and 50 pen enclosures (shrimp density=30 ind. m⁻²; current speed=0.001 m s⁻¹) on total nitrogen (TN) emission in Laguna de Rocha, calculated after Poersch (2006). Growth of shrimp individuals is also shown. The rapid increase of TN occurs mainly during harvest (showed as peaks in the graph), when sediments are removed to catch the buried shrimp. The horizontal line shows the TN acceptable limit.

containing many elements from the benthic community (e.g. benthic macrofauna, plant debris and detritus associated to macroalgae) have been observed by many authors (Dittel et al., 1997; Albertoni et al., 2003a), indicating that *F. paulensis* is omnivorous. Moreover, Albertoni et al. (2003b) observed that *F. paulensis* predaes on Tanaidacea, Ostracoda, *Heleobia australis*, Polychaeta, Isopoda, Chironomidae and Amphipoda. The impact on the benthic community caused by shrimp cultivation was also observed in Lagoa dos Patos by Poersch (2004). According to Soares et al. (2004), the total abundance of benthos organisms inside the pens in this lagoon diminished 86% after 21 days of cultivation. They reported predation by shrimp on Tanaidacea (*Kalliapseudes schubartii* and *Tanais stanfordi*), Polychaeta (*H. similis*, *N. fluviatilis* and *Laeonereis acuta*), Gastropoda (*Heleobia australis*), Isopoda (*Munna peterseni* and *Cassidinidea fluminensis*), Amphipoda (*Melita mangrovi*) and Bivalvia (*E. macroides* and *T. plebeius*).

3.3. Environmental sustainability and management

The simulation of the maximum number of pens that the lagoon can sustain while maintaining minimal environmental impact indicated that up to 13 pens can be installed in the Southern area of Laguna de Rocha (Fig. 4) without threatening the natural conditions of the system. At 13 pens, the simulated concentration of TN slightly exceeded the maximum acceptable limit of $760 \mu\text{g l}^{-1}$, (i.e. the average concentration of nitrogen observed in control sites during summer 2004 and commonly in the system), while at 50 pens the simulated value reached ca. 1 mg l^{-1} . Therefore if the number of pens installed in the lagoon exceeds the threshold number of 13 the water quality may be compromised, exceeding the capacity of the system to support shrimp cultivation in a sustainable manner.

Exceeding 13 pens would also bring about a reduction of the habitat area for benthos, interfering with other organisms like birds and fishes that feed on this community. However, this direct impact would be restricted only to the area occupied by the pens and only during the relatively short period of cultivation (3–4 months). Although our results suggest that an environmentally optimal number of 13 pens in Laguna de Rocha would assure the sustainability of natural processes and the potentiality to continue shrimp aquaculture in the lagoon, this initiative should be monitored and the results should be used to adjust the prediction model.

An additional consideration related to the sustainability of this aquaculture system (and the natural populations of pink shrimp in the coastal lagoons of Uruguay) is that post-larval shrimp can be vectors of viruses and diseases (e.g. “white spot”; Flegel et al., 1996). This is a major threat to commercial shrimp farms elsewhere (González et al., 2003) because viruses are also transported by water and intermediate crustaceans hosts (Funge-Smith and Briggs, 1998).

Even if the lagoon could sustain up to 13 pens without compromising the water quality, this figure may not guarantee the economical and social sustainability of the aquaculture initiative. Furthermore, there were drawbacks to this pilot project experience that should be improved in future trials with the aim of improving the economical benefits. For example, the timing of inoculation and harvest should be better synchronized with the high water temperature period to assure the optimal growth. The feeding frequency and food quality should also be adjusted to evade any food limitations, while invasion of pens by native crabs must be controlled to avoid competition for food.

These methodological shortcomings resulted in lower total production than expected; the total production calculated at the end of harvest was 280 kg. Nevertheless, the production was sold to two

exclusive restaurants at 5 US\$ per kg, double the normal price, because of the sanitary benefits of a programmed harvest in pens in comparison to traditional landings. Also, as this was the first pilot experience using this technology in Uruguay, the investment in larvae, equipment and technical support was covered by research funds. Therefore, the economical sustainability of the experience could not be properly evaluated (C. Fagetti, pers. comm.).

The organization of the fishing community in Laguna de Rocha is basically established by familiar links and a half-century fishing tradition, whereby activity is self-controlled by the natural carrying capacity of the lagoon (local fishermen, pers. comm.). Even if aquaculture production were economically sustainable, the potential arrival of new families could disturb the natural carrying capacity of the lagoon and could result in economic speculation by external enterprises or by the fishermen themselves. This could be partially avoided by keeping the number of pens the lowest possible and by assigning shrimp pens, through the administration authority, only to permanent fishermen.

In addition to these considerations, a permanent monitoring program must be conducted if sustainable aquaculture in the Atlantic coastal lagoons of Uruguay is to be further promoted. For this program we suggest a sampling design similar to the one exercised in the present study. The BACI design, a fine statistical analysis and modeling tools, proved to be a powerful, simple and low cost instrument for assessing the environmental impact of a new economic activity in a protected area.

Acknowledgments

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**Anexo III - Distribution of saltmarsh plant communities
associated with environmental factors along a latitudinal
gradient on the south-west Atlantic coast**

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Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast

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ABSTRACT

Aim To produce an inventory of south-west Atlantic saltmarshes (from latitude 31°48' S to 43°20' S) using remotely sensed images and field sampling; to quantify their total area; to describe the biogeographical variation of the main habitats characterized by dominant vascular plants, in relation to major environmental factors; to test the hypothesis of predominance of the reversal pattern in plant distribution (sedges and grasses dominate the lower, regularly inundated zones, while the upper zones are occupied by more halophytic species) previously described; and to compare these south-west Atlantic saltmarshes with others world-wide.

Location South-western Atlantic saltmarshes

Methods Field samples of dominant emergent plant species positioned by the global positioning system (GPS) were obtained from most coastal saltmarshes (14) between southern Brazil and northern Patagonia, Argentina. Landsat satellite images were obtained and coastal saltmarsh habitats were quantified by supervised classification, utilizing points gathered in the field.

Results Three main plant species dominated the low and middle intertidal saltmarsh, *Spartina alterniflora* Loesel., *Spartina densiflora* Brong. and *Sarcocornia perennis* (P. Mill.) A.J. Scott. The total area of the studied coastal saltmarshes was 2133 km², comprising 380 km² of *Sp. alterniflora* marsh, 366 km² of *Sp. densiflora* marsh, 746 km² of *Sar. perennis* marsh and 641 km² of brackish marsh (dominated by *Juncus acutus* L., *Juncus kraussii* Hochst., *Scirpus maritimus* L., *Scirpus americanus* Pers. and *Phragmites australis* (Cav.) Trin.). Cluster analysis showed three habitat types: saltmarshes dominated by (1) *Sp. densiflora* and brackish species, (2) *Sp. alterniflora* and *Sar. perennis* and (3) *Sp. densiflora* only. The analysis of abiotic variables showed significant differences between groups of habitats and coordinated gradients of the abiotic variables. The south-west Atlantic coast showed decreasing mean annual rainfall (1200 to 196 mm) and increasing mean tidal amplitude (< 0.5 to > 2.5 m) from latitude 31° to 43°.

Main conclusions South-west Atlantic saltmarshes are globally important by virtue of their total extent. Remote sensing showed that the reversal pattern in plant distribution is not widespread. Indeed, south-west Atlantic saltmarshes are better characterized by the presence of the halophytic genera *Spartina* and *Sarcocornia*. Our results support the interpretation that south-west Atlantic saltmarshes constitute a class of temperate type (*sensu* Adam, 1990) with transitional characteristics between Australasian–South African saltmarshes and west Atlantic saltmarshes.

Keywords

Argentina, Brazil, coastal saltmarsh, *Sarcocornia*, south-west Atlantic coast, *Spartina*, Uruguay, zonation.

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INTRODUCTION

Saltmarshes are intertidal ecosystems, backed up against the land on one side while open to the sea on the other (Wiegert *et al.*, 1981). They embody environmental characteristics of both terrestrial and marine communities. They are plastic coastal features, shaped by the interaction of water, sediments and vegetation. For stability, they require protection from high-energy waves and therefore usually develop in sheltered sites. In some parts of the world they show extremely diverse vegetation (boreal type *sensu* Adam, 1990), while in other regions they are dominated by a few plant species, usually grasses (west Atlantic type *sensu* Adam, 1990).

As for other continents (Adam, 2002), there is no reliable inventory of coastal saltmarsh area for South America. West (1977) pointed out that between southern Brazil and northern Patagonia (south-west Atlantic region) there are extensive saltmarshes on estuaries with large discharges and prevailing brackish conditions. An important feature of saltmarshes is variation in the species composition of vascular plants with elevation (Adam, 1990), but although these zonation patterns are also used for classification of coastal saltmarshes throughout the world (Adam, 1990), few syntheses of Latin American saltmarsh vegetation have been attempted (West, 1977; Costa & Davy, 1992). Early classifications of coastal saltmarshes of the world (Chapman, 1960) included the coasts of Argentina, Uruguay and the south of Brazil within a group denominated South American. West (1977) described zonation patterns that occur on a grand scale in these estuaries, where sedges and grasses dominate the lower, regularly inundated zones, and the upper zones are occupied by more halophytic species. Thus, although these marshes show affinities with temperate marshes elsewhere, based on the perception of an inverted zonation pattern, they have been recognized as a separate type (see Adam, 1990). However, descriptive studies of south-west Atlantic saltmarsh vegetation (Ringuelet, 1938; Chebataroff,

1952, 1953; Verettoni, 1961; Vervoort, 1967; Costa & Davy, 1992; Cagnoni & Faggi, 1993; Isacch, 2001; Costa *et al.*, 2003) and our observations suggest that the inversion of zonation pattern is restricted to small areas of the most extensive saltmarshes or to the upper estuaries of rivers influenced by fresh water. Therefore interpretation of the relationship between south-west Atlantic marshes with others world-wide is unclear.

The purpose of this work was to produce an inventory of south-west Atlantic coastal saltmarshes using a combination of remotely sensed images and field sampling. We aimed to quantify their total area and to describe regional variation of the main habitats characterized by dominant vascular plants, in relation to major environmental factors. We test the hypothesis of predominance of reversal in the pattern of plant distribution described by West (1977). This should enable comparison of south-west Atlantic coastal saltmarshes with others world-wide.

METHODS

Study area

The study area included coastal saltmarshes from southern Brazil (from 31°), Uruguay and Argentina (to 43° S; Table 1) including 14 different sites. This region has one of the widest and flattest continental shelves anywhere (the Southwest Atlantic Shelf) and it includes the coastal area of the confluence of the southward Brazil Current and northward Malvinas (Falkland) Current (Costa & Davy, 1992; Longhurst, 1998). The Subtropical Confluence occurs at the latitude of La Plata River, which generates an offshore flux whose location is seasonally variable and determined by the relative flux strengths of the two currents (Longhurst, 1998). From a terrestrial point of view, the study area crosses three large biogeographical provinces (Cabrera & Willink, 1973): Pampas

Table 1 Data of satellite imagery selected for the classification of coastal saltmarshes from Brazil, Uruguay and Argentina: L7, Landsat 7 (ETM+); L5, Landsat 5 (TM)

Site	Satellite	Path-row	Date	Latitude
Brazil				
Lagoa dos Patos	L7	221-82	12 November 2002	31°48'–32°11'
Uruguay				
Arroyo Maldonado	L7	222-84	18 March 2000	34°53'
Laguna José Ignacio	L7	222-84	18 March 2000	34°53'
Argentina				
Bahía Samborombón	L7	224-85	30 January 2001	35°13'–36°18'
Laguna Mar Chiquita	L5	223-86	3 February 2002	37°29'–37°46'
Bahía Blanca	L7	226-87	3 February 2003	38°41'–39°30'
Río Colorado	L7	226-88	15 January 2002	39°34'
Bahía Anegada	L7	226-88	15 January 2002	39°48'–40°42'
Río Negro	L7	226-88	30 October 2002	41°00'
Caleta de los Loros	L7	227-89	10 February 2003	41°01'
Bahía San Antonio	L5	228-88	5 January 2002	40°42'–40°50'
Riacho San José	L7	227-89	10 February 2003	42°24'
Caleta Valdés	L7	227-89	10 February 2003	42°15'–42°27'
Río Chubut	L7	227-90	10 February 2003	43°20'

	Mean tidal amplitude (m)	Run-off volume (m ³ s ⁻¹)	Annual rainfall (mm)	Phytogeographical province*
Brazil				
Lagoa dos Patos	0.47	2000†	1200	Pampas
Uruguay				
Arroyo Maldonado	0.31	14‡	1020	Pampas
Laguna José Ignacio	0.31	7‡	1020	Pampas
Argentina				
Bahía Samborombón	0.75	22,031§	950	Pampas
Laguna Mar Chiquita	0.79	20¶	920	Pampas
Bahía Blanca	2.44	–	645	Espinal and Pampas
Río Colorado	1.64	319§	600	Espinal and Monte
Bahía Anegada	1.64	–	500	Monte
Río Negro	2.94	858§	380	Monte
Caleta de los Loros	6.04	–	300	Monte
Bahía San Antonio	6.44	–	248	Monte
Riacho San José	3.00	–	225	Monte
Caleta Valdés	2.70	–	225	Monte
Río Chubut	2.77	47§	196	Monte

*After Cabrera & Willink (1973).

†Fernandes *et al.* (2002).

‡Unpublished report from the Ministerio de Transporte y Obras Públicas from Uruguay Conservación y Mejora de Playas. MTOP/PNUD/UNESCO, Report URU 73.007 (1979).

§Calcagno *et al.* (2000).

¶Estimated value after Fasano *et al.* (1982).

(dominated by grasslands), Espinal (dominated by thorn trees) and Monte (dominated by bushes) (Table 2). The annual mean precipitation increases from 250 mm in the south (Río Chubut) up to 1200 mm in the northern part of our study area (Lagoa dos Patos). Astronomical microtides (up to 0.5 m) on the southern Brazilian and Uruguayan coast contrast with meso-macrotides (2.7–6.4 m) dominating the coast to the south, in northern Patagonia. Sediments from saltmarshes of Argentina, Uruguay and Brazil have variable quantities of sand, shells and boulders, but mud always represents the highest percentage (Urien & Ewing, 1974; Fasano *et al.*, 1982; Calliari, 1998; Yorio, 1998). Light cattle grazing on coastal saltmarshes can occur at a low frequency (Bilenca & Miñarro, 2004; Isacch *et al.*, 2004).

Definition of main habitats and field sampling

Phytosociological studies have been carried out in southern Brazil (Reitz, 1961; Danilevicz, 1989; Costa, 1997), Uruguay (Chebataroff, 1952, 1953) and Argentina (Ringuelet, 1938; Parodi, 1940; Verettoni, 1961; Vervoort, 1967; Faggi, 1985; Cagnoni & Faggi, 1993) characterizing dominant taxa and their associated species. Since the south-west Atlantic is a warm temperate biogeographical transition zone, some elements of the flora are restricted to the north subtropical border (e.g. *Acrosticum* spp., *Paspalum vaginatum*) and others to the southern cold temperate zone (e.g. *Puccinellia* spp.). Nevertheless, regionally, consistent dominant taxa can be

Table 2 Physical factors and phytogeographical regions of the coastal saltmarshes from Brazil, Uruguay and Argentina

recognized as indicators of species assemblages clearly related to topography and salt stress (Costa, 1997; Yorio, 1998) and responsible for distinctive landscape habitat units. Previous studies of Isacch (2001) and Nogueira & Costa (2003) demonstrated that spectral channels in the visible and reflected infrared region of digital images allowed a clear delimitation of water, non-vegetated tidal flats, uplands and marsh vegetated habitats dominated by *Spartina alterniflora* Loesel., *Spartina densiflora* Brong., *Sarcocornia perennis* (P. Mill.) A.J. Scott and brackish marsh species.

There is no coherent systematic treatment of the flora of Latin America and so, along the Atlantic coast, *Sp. alterniflora* and *Sp. densiflora* have been variously classified into several varieties, different species and hybrids, mainly based on differences of certain inflorescence features (Mobberley, 1956; Cabrera, 1970). Similar taxonomic uncertainties and ambiguities are observed for *Sar. perennis* (Reitz, 1961; Natural Resource Conservation Service, 2004). In order to map and categorize consistently the saltmarsh habitats characterized by their dominant cover along the coasts of southern Brazil, Uruguay and Argentina we considered here *Sp. densiflora* Brong. to be synonymous with *Spartina montevidensis* Arech., *Sp. montevidensis* (Arech.) St. Yves, *Spartina patagonica* Speg. and *Spartina juncea* Willd. var. (Cabrera, 1970); *Sp. alterniflora* Loesel. considered synonymous with *Spartina brasiliensis* Raddi and *Spartina maritima* var. *brasiliensis* (Raddi) St. Yves (Cabrera, 1970); *Sar. perennis* (P. Mill.) A.J. Scott to be synonymous with *Sarcocornia fruticosa* (= *Salicornia fruticosa*

L.), *Salicornia ambigua* Michx., *Salicornia gaudichaudiana* Mog. and *Salicornia virginica* L. (Reitz, 1961; Natural Resource Conservation Service, 2004).

All 14 sites within the study area with patches of saltmarsh vegetation recognized by the Landsat image (spatial resolution 30×30 m) were sampled between December 2002 and March 2004. Because of the great variability of extent of marsh and the complex environmental gradients for salinity and topography among study sites, geolocated (global positioning system, GPS) point samples were selected following a stratified random sampling scheme (Manly, 1993). The number of samples at each site was proportional to the area of saltmarsh. Data were gathered by selecting quadrats of 1×1 m within each type of habitat. Totals of 230, 85 and 735 quadrats were recorded for the occurrence of dominant and associated species, and visually estimated canopy cover at sites located in Brazil, Uruguay and Argentina, respectively. All the range of vegetated and non-vegetated intertidal habitats was surveyed by walking and/or using small low-speed planes in some cases. Non-vegetated habitats were denominated by tidal flats. All marshes dominated by species of *Scirpus*, *Juncus*, *Cortaderia* and *Phragmites* species, commonly associated with freshwater input to saltmarshes (Adam, 1990; Costa, 1997; Haacks & Thannheiser, 2003), were considered brackish marshes. Additional information about associated species was obtained from bibliographic references.

Remote sensing analysis

Data acquisition

The satellite imagery used was recorded by the Landsat Thematic Mapper (TM) sensor on board Landsat 5, and the Enhanced Thematic Mapper-plus (ETM+) sensor on board Landsat 7. We selected only those images taken at the lowest tidal levels, when the whole marsh would have been exposed, from the pool of satellite images for each site. Images of different sites were obtained between March 2000 and February 2003 (see Table 1 for details).

Image pre-processing procedures

The satellite images were geocoded to a Gauss Kruger (Campo Inchauspe datum for Argentine images) or UTM (Yacaré datum for Uruguay images and WGS-84 datum for Brazil images) coordinate system using a first-order transformation and nearest-neighbour resampling. The pixel size after resampling was 30×30 m and the root-mean squared errors achieved were always lower than 1.5 pixels. We used field and map points for georeferencing. At a few sites where the access was difficult and thus GPS data were impossible to get, data were acquired from topographic maps (scale 1 : 50,000).

Classification procedure and accuracy assessment

We used a supervised classification to identify coastal saltmarsh habitats (Campbell, 2002) for all saltmarshes within

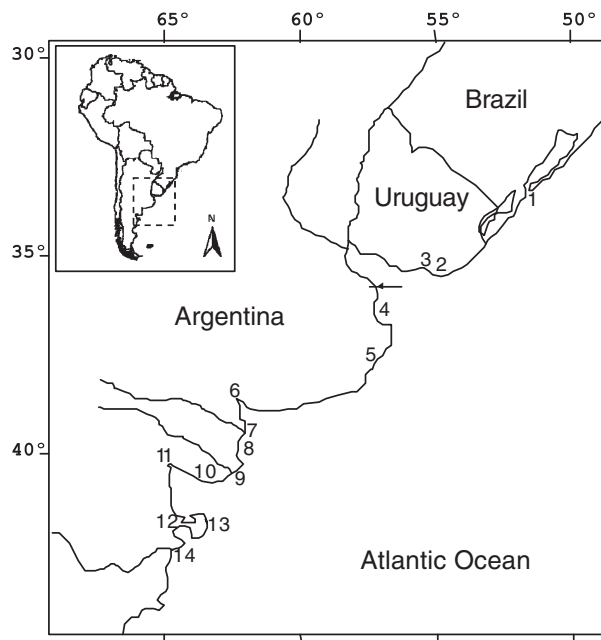



Figure 1 Saltmarshes of the south-west Atlantic coast. For details of sites (numbers) see Table 1. Arrow indicates Punta Indio.

the study area recognized by the spatial resolution of Landsat images (see Fig. 1). In this case we used one set of GPS points gathered in the field to generate the training sites, and the others were reserved to assess the accuracy of classifications. For the classification procedure we used a maximum likelihood probability algorithm (Richards, 1986), which is based on the probability density function associated with a particular training site signature. Pixels are assigned to the most likely class based on a comparison of the posterior probability that it belongs to each of the signatures being considered. The area of tidal flats and vegetated habitats from classified images for each saltmarsh were used for posterior analysis. We used an error matrix analysis to assess the accuracy of the classification procedure, using the kappa index of agreement and overall accuracy error (Rosenfield & Fitzpatrick-Lins, 1986). The number of reference test pixels used for the assessment of accuracy varied with the representatives of each class into the subset of the image (i.e. more cover more pixels). The environment of Idrisi 32 (Clark Labs, Worcester, MA, USA) was used for the analysis of satellite images.

Given that it may be difficult to detect the magnitude of zonation pattern directly from the classified satellite images, we designed a sampling scheme based on the satellite images. Using systematic sampling (Manly, 1993) of the classified satellite images, we sampled equidistant strips (vector lines) perpendicular to the coast of the marshes from the lower to the upper estuarine part of each site ($n = 30$; including all the gradient from saltwater-dominated to freshwater-dominated habitats to the upland border). Finally, the occurrence of a lower marsh halophytic–upper marsh brackish species zonation, or inverse zonation pattern (*sensu* West, 1977),

Table 3 Areas of different habitats from saltmarshes of the western south Atlantic coast, dominant species of brackish marsh and inverse zonation percentage (%). The kappa index of agreement and overall accuracy error for the classifications of saltmarshes habitats are also shown. Key: Sa, *Spartina alterniflora* Loesel.; Sd, *Spartina densiflora* Brong.; Sp, *Sarcocornia perennis* (P. Mill.) A.J. Scott; Sc, *Scirpus maritimus* L.; Se, *Scirpus americanus* Pers.; Jk, *Juncus kraussii* Hochst.; Ju, *Juncus acutus* L.; Co, *Cortadeira celloana* (Schult.) Asch. et Graeb.; Ph, *Phragmites australis* (Cav.) Trin. (+) Means recorded in the field but not with the satellite image analysis. (–) Means not recorded

	Surface covered (ha)					Species in brackish marsh	Inverse zonation (%)	Accuracy assessment		
	Sa marsh	Sd marsh	Sp marsh	Brackish marsh	Tidal flat			Kappa index (%)	Overall accuracy (%)	
Brazil										
Lagoa dos Patos	53	619	+	5551	+	Sc, Jk	3.3	75.1	86	
Uruguay										
Arroyo Maldonado	+	550	111	1222		+	Sc, Se, Ju	6.7	95.1	97.6
Laguna José Ignacio	–	178	2	469	+	Sc, Se, Ju	3.3	95.1	97.6	
Argentina										
Bahía Samborombón	5060	26314	8336	42345	14046	Sc, Ju, Co	6.7	76.5	94.8	
Laguna Mar Chiquita	–	3882	304	7382	143	Ju, Co	6.7	98.7	99.3	
Bahía Blanca	9193	65	20376	+	60973	Ju, Ph	0	83.4	97.9	
Río Colorado	397	1344	731	4548	1807	Ph	6.7	90.3	95.5	
Bahía Anegada	20503	2908	42060	2492	62797	Ph	0	90.3	95.5	
Río Negro	47	656	+	49	+	Ph	3.3	98.4	98.9	
Caleta de los Loros	440	+	30	–	1144	–	0	98.7	99.5	
Bahía San Antonio	2068	+	2124	–	10111	–	0	98.2	98.8	
Riacho San José	108	23	225	–	633	–	0	91.2	95.8	
Caleta Valdés	89	25	329	–	2747	–	0	91.2	95.8	
Río Chubut	–	18	+	–	+	–	0	87.7	94.8	

was assigned to each strip, and the frequency of inverse zonation patterns was estimated for each of the 14 sites.

Statistical analysis

The percentage coverage of tidal flats and vegetated habitats in each saltmarsh was used to classify sites in a clustering procedure. A Euclidean distance algorithm was used to calculate dissimilarity indexes between all pairs of saltmarshes (following Hair *et al.*, 1995). We also used a bootstrapping technique to identify statistically significant groups of sites (Jaksic & Medel, 1990). The cluster analysis procedure was repeated 1000 times for each of the new matrices generated with the bootstrapping technique (following Caswell, 1989). Each iteration gave six node values, and then from the resulting distribution of the 6000 pseudovalues (nodes) the program gave a cut-off threshold for significantly distant values. We chose the fifth percentile of the distribution of node values; therefore, habitat coverage groups of saltmarsh sites obtained at distance values lower than the cut-off ($P < 0.05$) were considered significantly different.

Discriminant analysis (Hair *et al.*, 1995) of standardized values of abiotic variables was used to test the hypothesis that the abiotic factors distinguished the groups of saltmarshes obtained by cluster analysis. Rainfall data were obtained from the US Department of Commerce, National Oceanic and Atmospheric Administration (NOAA), National Environmental Satellite, Data, and Information Service Office, National

Climatic Data Center (<http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html>). Freshwater run-off data were $\log_{10}(x + 1)$ transformed to increase homogeneity of variance and normality. The discrimination between centroids was tested at the 5% significance level by Wilk's lambda statistics and Rao's 'V' statistics, showing the multidimensional distance between groups of saltmarshes (Klecka, 1975).

RESULTS

Three main plant species dominated the low and middle intertidal saltmarshes of the coastal south-west Atlantic: *Sp. alterniflora*, *Sp. densiflora* and *Sar. perennis* (Table 3; Figs 2 & 3). *Spartina alterniflora* was always in the mid-intertidal (inundated by all high tides) oceanic front of the saltmarsh as monospecific stands. The other two species frequently occupied upper levels in the intertidal area (inundated mainly during spring high tides) and presented three different patterns: (1) *Sp. densiflora* only, (2) *Sar. perennis* only and (3) a mixture of *Sp. densiflora* and *Sar. perennis*. In these three types of saltmarsh stand other species mainly occupied a zone a few metres wide between *Sp. densiflora* and brackish marsh (Table 4), or were in the upper border of *Sar. perennis*-dominated marshes from Bahía Blanca to Río Chubut. In the area located at the upper part of *Sar. perennis* marshes from Bahía Blanca to Río Chubut, associated species were similar (*Heterostachys rytheriana* (Moq.) Ung. Stern, *Limonium brasiliensis* (Boiss.) O. Kuntze., *Atriplex* spp.,

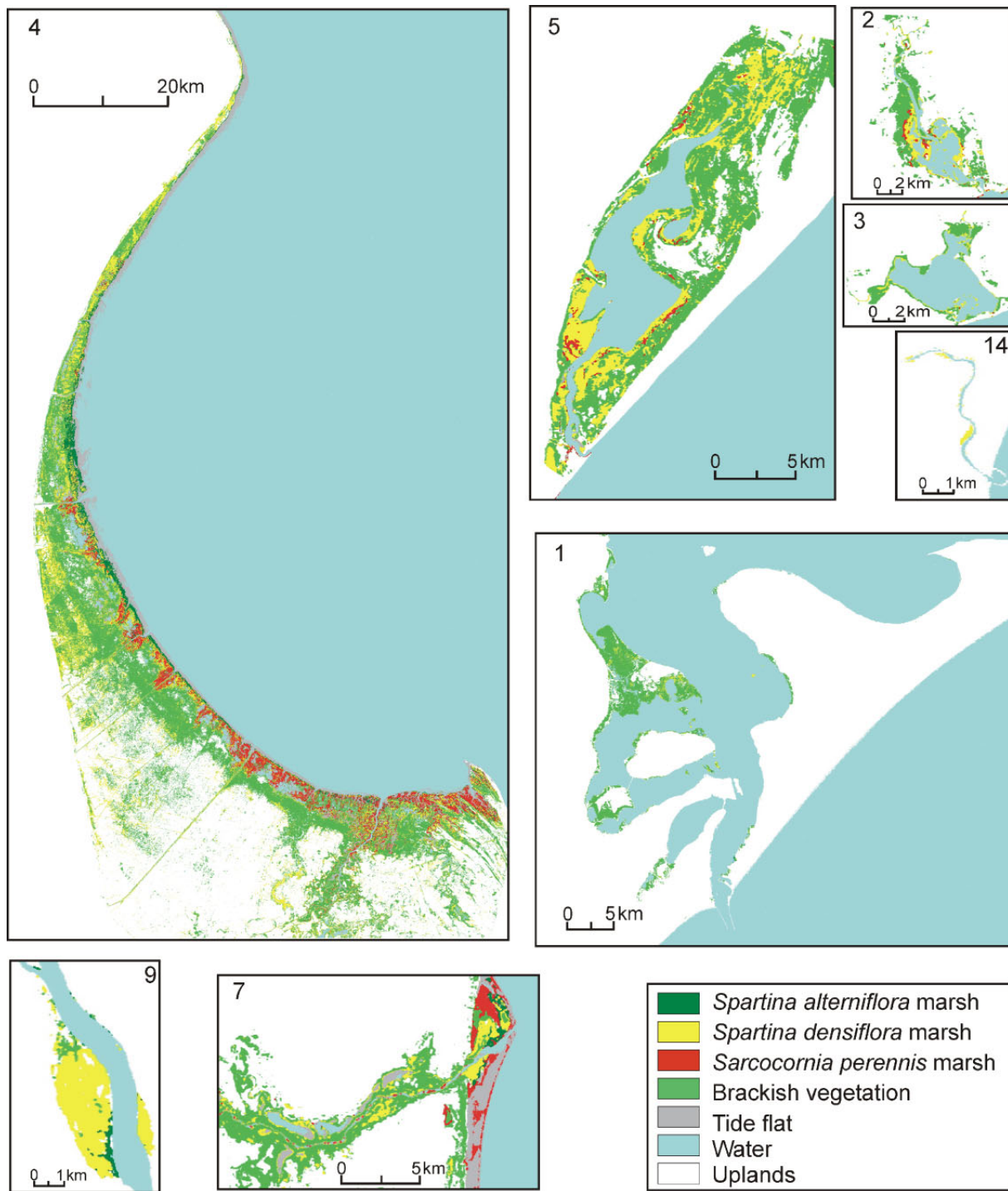


Figure 2 Saltmarshes of the south-west Atlantic coast characterized by the influence of freshwater. For references to sites (numbers) see Table 1.

Lycium chilensis Miers, *Suaeda patagonica* Speg., *Suaeda divaricata* Moq.; Verettoni, 1961; Yorio, 1998; and personal observation). Brackish vegetation was frequently recorded on the landward side of the three former species zones. Also, brackish marshes were found on the leading edge of saltmarshes with freshwater input, but always in the upper

estuarine part of rivers and coastal lagoons where the influence of fresh water was marked. Although inverse zonation patterns were recorded in a few saltmarshes with freshwater input, their frequency was lower than 7% (Table 3).

The total area covered by coastal saltmarshes in the studied area is 2133 km² (Argentina 2045 km², Uruguay 25 km²,

Table 4 The most common associated species present within *Spartina densiflora* marshes and brackish marshes for the different coastal saltmarshes of the south-west Atlantic characterized by the influence of fresh water

Region	Species	References
Brazil (Lagoa dos Patos)	<i>Scirpus maritimus</i> L., <i>Vigna luteola</i> (Jacq.) Benth., <i>Rumex paraguayensis</i> D. Parodi, <i>Aster squamatus</i> (Spreng.) Hier., <i>Paspalum vaginatum</i> Swartz, <i>Polygonum neglectum</i> L. and <i>Eclipta prostrata</i> (C.) Hassk.	Danilevicz (1989), Costa & Davy (1992), Costa (1997)
Uruguay (Arroyo Maldonado, Laguna José Ignacio)	<i>Scirpus maritimus</i> L., <i>Scirpus americanus</i> Pers., <i>Juncus acutus</i> L.	This study
Argentina (Bahía Samborombón, Laguna Mar Chiquita)	<i>Distichlis spicata</i> (L.) Green, <i>Apium leptophyllum</i> (Pers.) F. Muell., <i>A. sellowianum</i> Hoff, <i>Sarcocornia perennis</i> (P. Mill.) A.J. Scott, <i>Juncus acutus</i> L.	Cagnoni & Faggi (1993), Isacch <i>et al.</i> (2004)

Brazil 62 km²), 380 km² being dominated by *Sp. alterniflora*, 366 km² by *Sp. densiflora*, 746 km² by *Sar. perennis* and 641 km² by brackish marshes. The dominant brackish marsh species were *Juncus acutus* L., *Juncus kraussii* Hochst., *Scirpus maritimus* L., *Scirpus americanus* Pers., *Cortaderia selloana* (Schult.) Asch. et Graeb. and *Phragmites australis* (Cav.) Trin. (Table 3). Additionally, the total area of non-vegetated tidal flats at low tide was 1544 km².

Cluster analysis and bootstrap procedures identified three significantly distinct coverage groups of saltmarsh habitat (Fig. 4). The first group (all northern marshes between Lagoa dos Patos and Laguna Mar Chiquita and also the Río Colorado) was characterized by the dominance of *Sp. densiflora* at the oceanic leading edge of the marshes and brackish marshes covering the inland border (Fig. 2). The second group (marshes between Bahía Blanca and Caleta Valdés) was composed of *Sp. alterniflora* low marshes and *Sar. perennis* upper marshes (Fig. 3). The third group (Río Negro and Río Chubut) included saltmarshes where *Sp. densiflora* spread over most of the intertidal zone, either monospecifically or associated with a few other species (Fig. 2).

The analysis of abiotic variables showed significant differences between habitat coverage groups for saltmarshes and correlated gradients between the abiotic variables (Table 5, Fig. 5a). The main coordinated gradient was identified by the abiotic discriminant function 1 (AF1). AF1 was positively correlated with latitude and mean tidal amplitude of the saltmarshes and negatively correlated with mean annual rainfall (Table 5). The south-west Atlantic coast showed decreasing mean annual rainfall ($r^2 = 0.95$, $n = 14$, $P < 0.001$) and an increasing mean tidal amplitude ($r^2 = 0.45$, $n = 14$, $P = 0.009$) from latitude 31° to 43° S (Fig. 5). The AF1 discriminated both southern marsh groups 2 and 3 from the northern group 1 (Figs 4 & 5a). Groups 2 and 3 were separated by AF2, which described the significant ecological effect of freshwater run-off into the dry southern coast, differentiating Río Negro and Río Chubut saltmarshes from the others (Table 5, Fig. 5a). Together the discriminant functions AF1 and AF2 accounted for 100% of the explained

variance and classified the saltmarshes with 100% accuracy. Differences in the area covered by dominant saltmarsh plants identified abiotically distinct sites, characterized by decreasing annual rainfall, increasing latitude and mean tidal amplitude (Fig. 5a–c).

DISCUSSION

Our study combined field data and remote sensing technology to generate an inventory of south-west Atlantic coastal saltmarshes. These procedures have already been used to survey and classify saltmarsh habitats (see Klemas, 2001), Landsat TM and ETM+ being the most widely used satellites to identify vegetation types, because of their high-quality data for these targets (Campbell, 2002). TM satellites are able to separate salt-marsh vegetation communities (Donoghue & Shennan, 1987) and identify brackish water marshes (Bailey, 1997; Zhang *et al.*, 1997), although Landsat sensors had some difficulty in classifying the vegetation types of brackish marshes. Recently, there have been studies using remote sensors with higher spatial resolution to identify saltmarsh habitats (Bajjouk *et al.*, 1996; Eastwood *et al.*, 1997; Smith *et al.*, 1998; Silvestri *et al.*, 2002), which unfortunately are expensive and available for few sites in South America. However, because of the extensive area cover by south-west Atlantic marshes, we are confident that the spatial resolution (30 × 30 m) of Landsat TM and ETM+ sensors provides a very reliable tool.

Our inventory demonstrates that south-west Atlantic coastal saltmarshes are globally important by virtue of their great extent (Table 6). Buenos Aires Province, in Argentina, includes 93% of the total saltmarsh area surveyed and the three main sites of Bahía Samborombón, Bahía Blanca and Bahía Anegada together represent 84% of the total inventory. Only the first of these sites has important freshwater input and the other two are associated with coasts containing extensive tidal flats with an average annual rainfall of less than 600 mm.

The south-west Atlantic coastal saltmarshes are diverse from a geomorphological standpoint; they develop on areas dom-

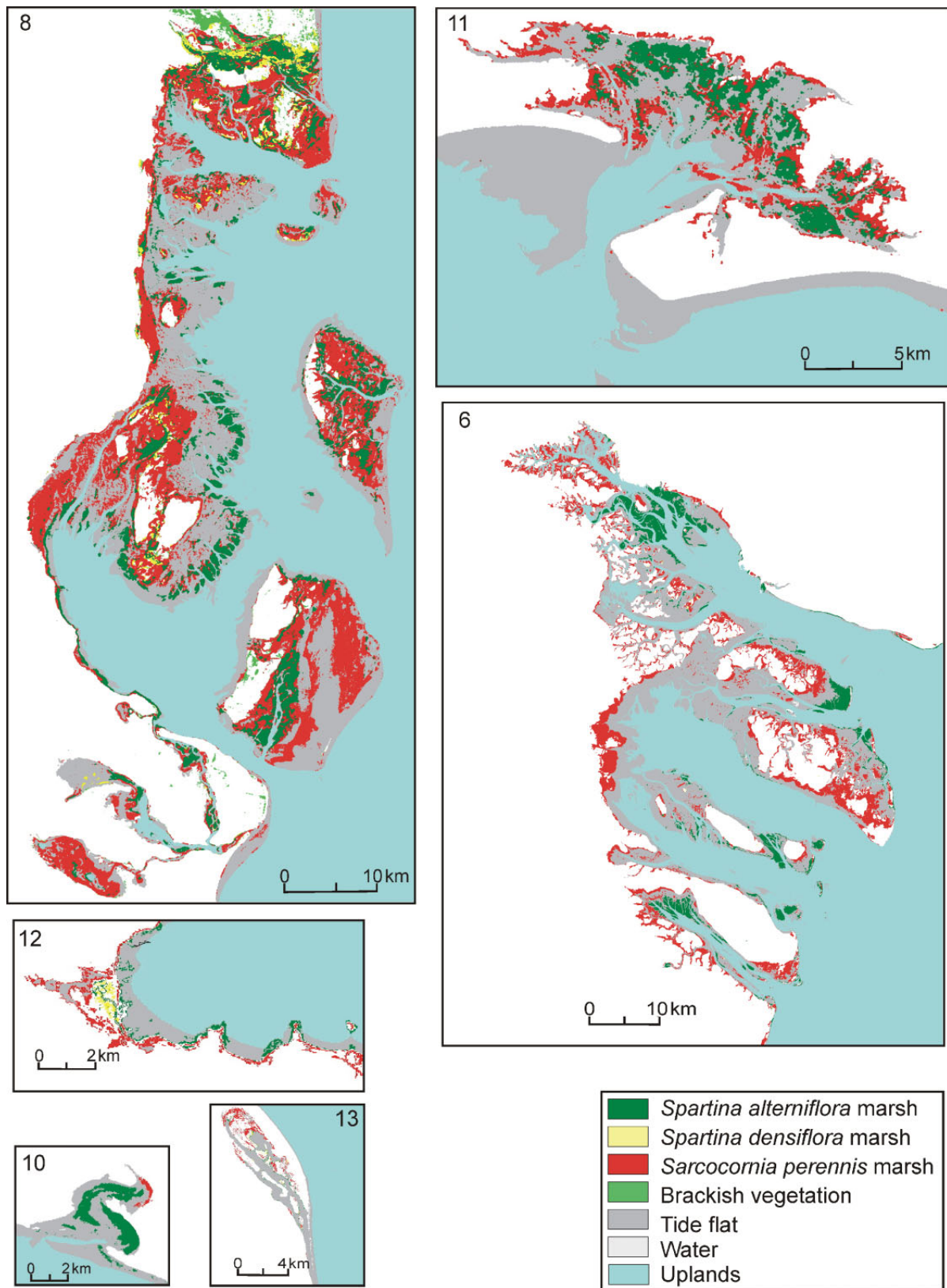


Figure 3 Saltmarshes of the south-west Atlantic coast characterized only by the influence of seawater. For references to sites (numbers) see Table 1.

Table 5 Abiotic discriminant analysis of the habitat coverage groups of coastal saltmarshes of the south-west Atlantic. Significant discriminant function, explained variance, correlation coefficients (*R*) and the canonical discriminant functions of the abiotic variables that discriminated the habitat coverage groups are shown. Wilk's lambda = 0.086, $F_{8,16} = 4.839$, $P < 0.004$

d.f.	Explained variance (%)	Abiotic variables	<i>R</i>	Canonical discriminant functions	
				Root 1	Root 2
1	83.4	Latitude	0.860	-1.052	0.930
		Annual rainfall	-0.922	-1.732	0.134
		Mean tide	0.822	-0.029	-0.145
2	16.6	Run-off volume	0.546	-0.610	0.843

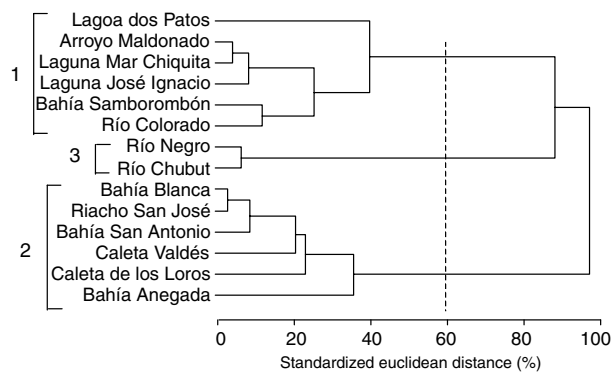


Figure 4 Unweighted Pair Group Method with Arithmetic Mean (UPGMA) distance dendrogram from cluster analysis of 14 saltmarsh sites based on the percentage of cover of different habitats. The vertical line was obtained from a bootstrap procedure and indicates that groups of sites to the left of the line are significant at $P < 0.05$. Numbers (1–3) represent different habitat coverage groups.

inated by tidal flats of rivers, lagoons, creeks, coves and bays. However, three groups of habitat coverage can be identified. Two major habitat coverage groups were separated geographically; brackish and marine waters dominate the northern and southern parts, respectively, of the latitudinal gradient studied. Brackish waters are related to areas of high rainfall (mostly 920 to 1200 mm year⁻¹) and estuarine regions of large watersheds (Costa & Davy, 1992; Costa *et al.*, 2003). The southern part is characterized by low rainfall (< 650 mm year⁻¹) and the presence of large bays, some of them originating from extinct or almost extinct large rivers (e.g. Río Colorado; Spalleti & Isla, 2003). Dry coastal areas with a mean freshwater input of 50–850 m³ s⁻¹ and mesotides (Río Chubut and Río Negro) produce a third group that has intermediate characteristics. In contrast to the conclusion of West (1977) the southern part of the south-west Atlantic coast is dominated by typical saltmarsh vegetation. Indeed, *Sp. alterniflora*, *Sp. densiflora* and *Sar. perennis* cover dominates 70% of saltmarshes of the south-west Atlantic coast.

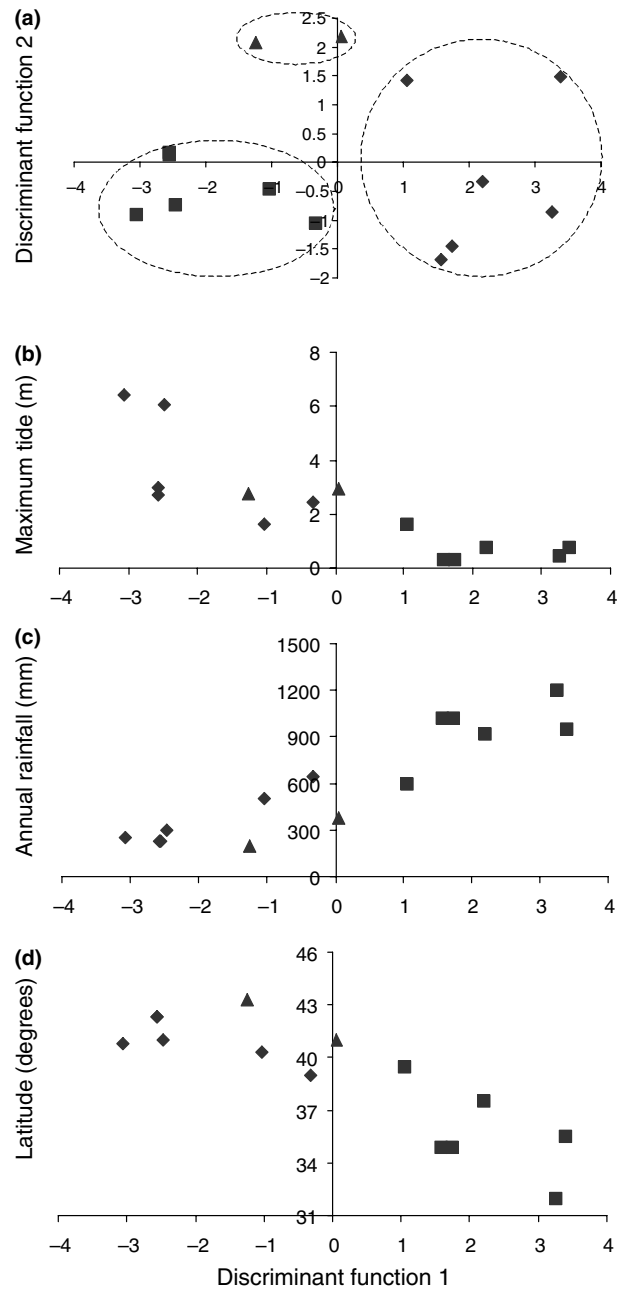


Figure 5 (a) Ordination of coastal saltmarshes of the south-west Atlantic according to the abiotic discriminant functions (DF) and relationship between DF1 and (b) latitude, (c) annual rainfall and (d) mean tidal amplitude for 14 saltmarshes of southern Brazil, Uruguay and Argentina. Similar symbols indicate saltmarshes from the same habitat coverage group. Squares, diamonds and triangles represent sites from groups 1, 2 and 3 listed in Fig. 4, respectively.

Biogeographical variation of saltmarshes along a large latitudinal range has also been recognized by Chapman (1960) and Adam (1990) for the North American west Atlantic saltmarshes, but has mainly been interpreted as the result of differences in solar energy received. Considering the dominant species and the floristic species, both authors distinguish a cold

Table 6 Area of saltmarsh for large regions of the world

Region	Tidal marsh area (km ²)	Reference
Gulf Coast (North America)	9880	Field <i>et al.</i> (1991)
Atlantic coast (North America)	5000–6000	Field <i>et al.</i> (1991)
Pacific coast (North America)	440	Field <i>et al.</i> (1991)
British Isles	450	Dijkema (1990)
Western Europe	950	Dijkema (1990)
Australia	6020*	N. Montgomery, OzEstuaries (pers. comm.)
South-west Atlantic coast (Brazil, Uruguay and Argentina)	2133	This study

*That value includes saltmarshes and salt flats (N. Montgomery, OzEstuaries pers. comm.).

temperate northern type (e.g. the Bay of Fundy) and a warm temperate–subtropical coastal plain (southward from North Carolina). Similar changes of solar radiation or temperature seem not to be responsible for observed biogeographical changes in south-west Atlantic marshes, since the low-latitude dominant species *Sp. densiflora* is able to withstand lower average temperatures than *Sp. alterniflora* (southern dominant species). The southernmost populations of *Sp. densiflora* and *Sp. alterniflora* are found at Río Gallegos (51° S; West, 1977) and Valdés Peninsula (42° S, this study) where average temperatures are 12–1 °C (summer–winter) (Faggi, 1985) and 18–7 °C (summer–winter) (Paruelo *et al.*, 1998), respectively. Consequently, the dominance or co-dominance of *Sp. alterniflora* and *Sar. perennis* along most of the northern Patagonian coast seems related to the prevalence of euhaline conditions and is not explained by the latitudinal variation of temperature or radiation.

A marked gradient of increasing aridity and tidal amplitude can be observed from southern Brazil (31° S) to the Valdés Peninsula (43° S) and is associated with changes of the saltmarsh communities. Two large groups of coastal saltmarshes are recognized, and their boundary occurs between Laguna Mar Chiquita and Bahía Blanca (approximately between 38° S and 39° S). This coincides with the limit between the Pampas and Espinal–Monte biogeographical provinces described by Cabrera & Willink (1973), which are characterized by decreasing rainfall southward. In the northern part of this region, the coastal brackish water marshes of the Lagoa dos Patos and Río de la Plata estuaries are dominated by mixed and monospecific stands of *Sp. densiflora* (Cagnoni & Faggi, 1993; Costa, 1997; Costa *et al.*, 2003), whereas in the southern part seasonally hypersaline semi-arid bays are dominated by *Sp. alterniflora* and *Sar. perennis*. The large low-energy flats in the southern part also facilitate colonization by *Sp. alterniflora* of the low intertidal area that is flooded by all tides (Adam, 1990), while *Sp. densiflora* and/or *Sar. perennis* dominate the upper marshes (Yorio, 1998). The existence of an intermediate group in middle latitudes (*Sp. densiflora*-domin-

ated marshes between 41 and 43° S; at Río Negro and Río Chubut) shows the determinant forcing factor of freshwater input on south-west Atlantic saltmarshes. Monopolization by *Sp. alterniflora* of those estuarine intertidal areas dominated by seawater may not only be a question of salt tolerance. A recent reciprocal transplantation experiment in southern Brazil showed that *Sp. densiflora* is highly competitive in irregularly flooded estuaries subjected to marked freshwater discharge extending over low and middle marshes (Costa *et al.*, 2003). Elsewhere it has been demonstrated that biological interactions between saltmarsh plants are sensitive to numerous aspects of the physicochemical environment and this may affect their relative distributions (Adam, 1990, 2002).

The northern part of the study site is the coastal area of the large Pampas plains (Soriano *et al.*, 1991). The dominant landforms are lowlands characterized by saline soils. However, small coastal areas may show the local influence of freshwater conditions, producing local inverse patterns in plant zonation. In these areas, halophytic vegetation may grow in the upper marsh and inland while freshwater marsh vegetation may dominate the low tidal marsh. The inverse pattern cited by West (1977), following Parodi, 1940) corresponds with a particular site of the Río de la Plata coast (Punta Indio, 37°16'24" S 57°13'34" W; Fig. 1). Following West (1977), Adam (1990) assumed that, in spite of the affinities with temperate types, a widespread reversal of zonation pattern in south-west Atlantic marshes makes them a different biogeographical group. However, remote sensing showed that the inverse zonation patterns are not widespread. Indeed, south-west Atlantic saltmarshes are better characterized by the presence of the halophytic genera *Spartina* and *Sarcocornia*.

The present results support the interpretation that south-west Atlantic saltmarshes constitute a group of the temperate type (*sensu* Adam, 1990) with transitional characteristics between Australasian–South African saltmarshes (*Sarcocornia* spp. in the lower marshes and *J. kraussii* in the upper marshes; Congdon, 1981; Adam, 2002; Haacks & Thannheiser, 2003) and west Atlantic saltmarshes that extend along Atlantic coast of North America and the Gulf of Mexico (dominance of *Sp. alterniflora*; Wiegert *et al.*, 1981; Day *et al.*, 1989; Adam, 1990, 2002). Additionally, south-west Atlantic saltmarshes have as a unique characteristic the presence of extensive upper marsh areas covered by the South American cord grass *Sp. densiflora*.

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BIOSKETCHES

Juan P. Isacch's research is focused on the use of remote sensing to study large-scale ecological patterns in coastal ecosystems.

César S. B. Costa's research interests are plant population dynamics and community structure.

Lorena Rodríguez-Gallego works on the ecology of macrophytes and the impact of land use changes on the trophic state of coastal lagoons.

Daniel Conde studies aquatic primary productivity and ecosystem processes in coastal lagoons.

Mauricio Escapa is interested in the role of biological interactions in the community structure and geomorphology of coastal salt marshes.

Domingo A. Gagliardini's main area of research is the application of remote sensing in coastal regions.

Oscar O. Iribarne works on ecological processes in coastal ecosystems.

Editor: Pauline Ladiges

Anexo IV

Matrices de datos

Laguna del Diario

Fecha	Estación	PO4 ug/l	PT ug/l	SI ug/l	NH4 ug/l	NO2 ug/l	NO3 ug/l	NID ug/l	NT ug/l	SS mg/l	%MOss	%MOsed	PTsed ug/gPS	NTsed ug/gPS	Cla fito ug/l	Cla fitobento	Z m	OD mg/l	K mS/cm	T °C	pH	KD m
09/02/2005	1	28.2	37.3	1900.5	9.3	0.3	22.3	31.9	517.6	3.9	69.9	9.1	486.9	351.1	1.1	40.5	1.4	7.4	0.5	22.5	8.1	2.1
09/02/2005	2	25.9	35.1	1762.4	29.2	1.0	22.9	53.1	587.0	14.9	73.1	9.6	403.6	315.2	1.8	54.1	1.5	7.2	0.5	22.5	8.1	1.8
09/02/2005	3	22.3	34.0	1841.6	17.5	1.5	21.6	40.6	717.3	1.7	66.7	13.2	628.5	445.9	2.3	21.6	1.4	7.1	0.5	22.8	8.1	2.4
09/02/2005	4	20.3	35.7	1335.2	16.2	0.1	22.2	38.5	863.1	5.6	60.0	10.8	594.1	226.7	3.0	88.8	1.7	8.5	0.6	23.8	8.2	2.6
09/02/2005	5	21.8	38.5	1374.6	30.0	0.5	23.4	53.8	551.4	7.2	61.1	11.1	559.7	302.9	2.2	91.9	1.8	8.6	0.6	23.3	8.2	1.4
09/02/2005	6	21.0	33.7	1193.1	35.5	0.6	23.4	59.5	456.2	3.2	60.6	11.6	405.3	224.8	2.6	19.2	1.7	8.9	0.5	23.7	8.1	2.5
02/05/2005	1	44.4	68.7	3890.7	95.9	3.9	0.0	99.8	519.7	40.7	13.6	8.6	280.3	564.9	1.9	11.3	1.4	10.3	0.4	17.0	8.4	4.6
02/05/2005	2	46.9	78.9	4008.9	0.0	4.5	0.0	4.5	630.0	24.1	53.8	9.3	338.7	867.9	0.6	29.4	1.4	9.2	0.3	17.1	8.5	4.8
02/05/2005	3	47.4	75.0	4570.4	0.0	7.8	0.0	7.8	581.2	22.1	26.7	13.0	406.6	1199.2	2.7	15.2	1.4	8.9	0.3	17.3	8.3	5.1
02/05/2005	4	43.2	79.3	4275.7	0.0	15.6	0.0	15.6	1075.6	32.9	43.5	10.6	186.6	362.0	6.1	11.7	1.6	9.7	0.4	18.3	8.2	4.8
02/05/2005	5	44.3	77.7	4415.9	0.0	6.2	0.0	6.2	883.7	22.9	62.5	11.3	333.3	696.5	8.6	55.6	1.8	9.5	0.4	17.4	8.1	4.7
02/05/2005	6	42.5	75.7	3623.1	0.0	10.1	0.0	10.1	866.7	31.0	44.4	10.4	365.9	773.1	6.1	56.8	1.7	9.6	0.4	17.7	8.2	3.9
02/08/2005	1	2.7	31.0	2815.9	13.7	1.0	4.4	19.1	450.8	22.0	33.3	11.0	700.8	2828.6	1.0	30.0	1.5	9.1	1.1	16.7	7.6	2.4
02/08/2005	2	2.3	38.4	2551.5	25.2	1.4	0.0	26.6	678.1	34.2	51.9	9.8	749.2	2026.0	0.4	15.8	1.5	9.3	1.1	16.3	7.6	2.7
02/08/2005	3	1.3	41.8	1796.5	0.0	1.1	0.0	1.1	184.1	36.3	34.5	9.0	740.8	2270.0	1.6	49.3	1.5	8.3	1.2	17.5	7.5	2.9
02/08/2005	4	4.8	46.6	2140.9	0.0	1.3	0.0	1.3	514.5	32.5	42.3	13.8	1088.6	3516.2	0.3	21.0	1.7	8.3	1.2	17.1	7.6	2.6
02/08/2005	5	4.8	41.3	2555.0	0.0	1.9	0.0	1.9	260.1	36.0	22.2	12.5	888.0	2664.6	0.1	18.6	1.8	8.5	1.2	16.7	7.7	2.8
02/08/2005	6	5.2	36.3	3409.7	0.0	1.4	0.0	1.4	319.6	30.7	13.0	14.7	1135.4	3606.5	1.3	59.2	1.8	8.8	1.2	16.9	7.5	2.6
2-6/11/2005	1	3.3	25.4	1490.7	0.0	0.0	13.2	13.2	1125.1	7.9	90.9	11.6	749.9	2308.3	1.4	37.0	1.5	8.9	0.9	20.0	7.8	2.4
2-6/11/2005	2	0.0	28.7	1431.5	119.9	0.0	11.9	131.8	1145.7	11.3	72.2	11.6	595.4	2488.8	1.1	350.9	1.6	7.9	0.9	19.3	7.7	1.4
2-6/11/2005	3	4.0	30.3	1381.5	55.7	0.1	13.5	69.2	971.3	11.7	81.0	11.2	609.8	2480.7	1.4	31.4	1.5	7.7	0.9	19.7	7.6	2.2
2-6/11/2005	4	6.2	30.7	1885.0	0.0	0.1	13.8	13.9	1100.3	8.9	15.2	12.5	785.8	2281.1	1.7	32.0	1.8	7.9	1.0	19.7	7.6	1.2
2-6/11/2005	5	6.8	30.7	1396.0	0.0	0.0	10.3	10.3	1037.8	7.8	42.9	12.5	672.3	1768.1	1.7	44.7	1.8	7.7	1.0	19.7	7.5	1.3
2-6/11/2005	6	6.6	31.5	1667.8	0.0	0.0	46.0	46.0	1192.8	3.5	12.7	12.7	785.6	2685.6	1.4	47.0	1.9	7.4	0.9	19.9	7.5	1.4
09/02/2006	1	52.8	64.5	1067.5	81.3	0.0	22.3	103.6	517.6	7.7	69.9	13.1	612.7	3494.6	2.1	73.0	1.1	1.2	20.9	7.3	2.0	
09/02/2006	2	45.9	53.3	1778.5	28.5	0.0	22.9	51.4	587.0	15.0	20.0	8.6	489.0	2673.8	2.2	21.0	1.2	8.2	1.2	21.3	7.4	2.0
09/02/2006	3	53.5	72.0	1444.6	27.7	0.0	21.6	49.3	717.3	11.6	34.6	11.6	456.8	2530.4	0.6	93.8	1.2	8.5	1.2	21.7	7.4	1.5
09/02/2006	4	13.3	21.9	703.9	22.8	0.0	22.2	45.1	863.1	13.3	27.5	11.2	381.4	2438.6	2.4	17.7	1.4	10.6	1.4	22.8	7.4	0.8
09/02/2006	5	24.9	39.8	1235.0	25.4	0.0	23.4	48.8	551.4	10.6	25.9	10.6	561.1	2264.4	1.1	51.5	1.5	9.3	1.8	22.2	7.5	1.9
09/02/2006	6	21.0	25.5	575.2	19.9	0.0	23.4	43.3	456.2	5.1	60.6	10.7	387.3	2359.6	0.5	16.2	1.6	7.0	2.0	22.1	7.4	0.9
20/06/2006	1	10.0	11.3	1252.8	2.7	0.3	16.7	19.7	529.1	2.7	12.7	12.7	210.5	1513.3	0.7	18.1	1.8	11.2	1.0	12.8	9.3	5.9
20/06/2006	2	9.0	9.0	1294.7	0.0	0.2	14.7	14.8	458.5	2.7	15.9	15.9	255.4	1607.5	0.8	18.1	1.6	14.1	1.0	13.0	9.5	6.7
20/06/2006	3	9.6	9.6	1181.2	0.0	0.2	14.3	14.5	425.9	2.7	10.4	10.4	153.7	1286.4	0.8	73.5	1.6	12.1	10.4	13.0	9.5	6.8
20/06/2006	4	4.0	4.1	739.7	0.0	0.1	15.1	15.2	463.2	3.0	66.7	14.8	265.7	2119.7	11.0	84.3	1.8	15.3	1.3	14.0	9.9	5.3
20/06/2006	5	4.2	14.4	667.4	0.0	0.0	11.7	11.7	508.8	3.0	58.3	14.6	619.3	1696.9	18.0	28.8	2.0	15.2	1.3	13.9	10.0	5.5
20/06/2006	6	2.7	2.7	517.4	0.0	0.0	12.9	12.9	649.3	2.0	50.0	15.1	370.7	1843.4	3.2	116.0	1.9	15.3	1.3	14.5	10.0	5.7

Fecha		Laguna José Ignacio																		pH		KD m
Fecha	Estación	PO4 ug/l	PT ug/l	SI ug/l	NH4 ug/l	NO2 ug/l	NO3 ug/l	NID ug/l	NI ug/l	SS mg/l	%MOss	%MOard	PTsed ug/gP	NTsed ug/gP	Cla fito ug/l	Cla fitobento	Z m	OD mg/l	K m/Sicm	T °C	pH	KD m
16/02/2005	1	19.6	43.4	2502.28	31.8	1.44	0.00	33.22	610.56	75.0	14.7	2.34	214.5	108.2	6.1	19.2	0.35	10.03	34.8	23.8	7.91	3.558
16/02/2005	2	17.9	35.7	2889.32	43.2	1.82	0.00	44.97	708.63	23.5	29.8	2.49	208.4	128.7	3.8	58.9	0.35	8.8	36.9	23.8	7.85	1.679
16/02/2005	3	17.6	25.7	2643.48	56.8	0.86	0.00	57.67	31.71	16.8	33.3	1.12	98.9	22.1	2.8	25.2	0.3	8.31	35.7	23.7	7.86	1.235
16/02/2005	4	15.4	25.4	2712.77	40.1	1.61	0.00	41.67	16.33	17.6	27.3	3.36	229.2	107.3	2.7	27.9	0.45	8.44	33.1	22.4	7.85	0.819
16/02/2005	5	15.0	23.1	3238.40	35.8	1.29	0.00	37.14	71.89	32.1	31.1	3.07	230.4	94.1	3.0	43.0	0.45	8.2	32.1	23.2	7.9	1.383
16/02/2005	6	15.2	22.7	3187.54	35.9	1.53	0.00	38.41	99.37	26.5	27.5	2.90	83.3	46.4	3.1	21.6	0.3	7.3	22.8	22.8	7.93	2.021
16/02/2005	7	13.3	26.6	2520.55	21.2	1.84	0.00	23.07	116.11	20.8	40.4	0.96	111.4	49.9	0.9	43.0	0.4	9.93	35.6	22.4	7.99	0.669
16/02/2005	8	11.3	16.1	2106.46	23.5	1.03	0.00	24.54	0.00	9.7	26.5	2.21	170.4	73.1	1.1	54.0	0.4	10.12	35.5	25.1	8.01	0.954
16/02/2005	9	17.0	29.3	2612.63	13.0	1.79	0.00	14.74	73.40	17.3	25.0	1.07	118.5	21.6	0.8	19.1	0.35	10.1	36.5	24.4	8.03	0.707
16/02/2005	10	17.3	28.7	2739.35	32.5	1.76	0.00	34.30	179.67	19.3	24.1	1.18	159.4	48.0	3.3	33.2	0.4	9.77	36.6	25.4	8.17	0.854
16/02/2005	11	17.2	30.7	2702.09	27.2	1.67	0.00	28.90	82.62	17.3	38.5	0.83	90.1	48.0	3.3	15.2	0.3	8.89	36.4	24.5	8.21	1.121
16/02/2005	12	21.1	35.3	2168.87	46.8	1.21	0.00	48.02	215.21	14.3	44.0	1.12	141.7	28.2	1.8	23.3	0.3	10.4	36.8	22.3	8.11	0.969
02/05/2005	1	12.4	27.8	725.35	0.0	0.89	0.00	0.89	116.11	21.3	73.5	5.36	199.2	45.0	2.5	100.4	0.28	12.32	21.8	18.3	7.7	1.907
02/05/2005	2	13.7	34.8	941.06	0.0	1.03	0.00	1.03	127.04	20.5	65.9	4.67	158.2	50.1	3.5	66.1	0.28	11.77	21.2	17.6	7.82	1.496
02/05/2005	3	13.8	38.5	1202.09	0.0	1.26	0.00	1.26	174.20	15.9	82.1	4.66	173.8	99.0	1.4	55.8	0.28	12.13	21.1	17.6	7.81	1.375
02/05/2005	4	16.1	31.6	3091.74	24.4	1.44	0.00	25.84	74.42	23.7	2.28	173.7	182.4	0.7	20.1	0.2	8.16	4.66	18.7	8.05	3.620	
02/05/2005	5	18.4	26.9	3818.37	43.7	1.44	0.00	45.10	154.04	17.1	1.08	74.0	130.2	0.7	19.8	0.2	8.97	9.67	16.9	8.16	3.348	
02/05/2005	6	15.4	21.2	3686.90	31.4	1.50	0.00	32.85	79.21	32.5	0.95	91.8	82.7	0.7	30.6	0.15	9.94	8.71	17.8	8.26	0.730	
02/05/2005	7	16.4	19.9	1904.99	23.6	1.06	0.00	24.70	0.00	12.7	0.81	83.8	98.4	0.0	37.0	0.25	10.68	17.54	16.6	7.76	1.499	
02/05/2005	8	21.7	36.2	3018.89	52.2	1.61	0.00	53.83	310.88	17.3	96.2	0.30	74.1	102.1	1.4	22.0	0.23	10.44	17.68	19.4	7.75	0.898
02/05/2005	9	14.6	19.5	1708.03	28.8	1.29	0.00	30.05	19.75	14.0	0.98	85.5	28.3	0.7	12.7	0.25	10.6	16.72	18.9	7.72	0.619	
02/05/2005	10	30.7	33.0	1086.53	0.0	2.34	0.00	2.34	5.06	7.2	0.26	32.9	5.2	3.7	6.1	0.45	10.73	29.2	18.5	7.49	0.376	
02/05/2005	11	28.0	28.0	1115.24	0.0	2.25	0.00	2.25	19.07	8.0	0.74	71.4	33.4	2.1	18.9	0.33	10.27	29.4	19.5	7.44	0.900	
02/05/2005	12	45.3	52.7	1454.08	14.2	2.28	0.00	18.31	84.33	14.9	97.1	0.95	132.9	22.4	0.7	34.9	0.15	9.94	20.7	19.9	8.11	1.139
02/08/2005	1	0.0	26.9	844.28	0.0	0.35	0.00	0.35	380.42	26.1	36.1	4.15	364.8	1204.4	5.2	71.5	0.25	8.57	15.9	18.3	6.74	3.084
02/08/2005	2	0.0	19.4	2489.77	40.0	0.00	0.00	39.98	167.89	26.7	30.6	3.10	411.1	928.5	5.7	33.9	0.3	8.9	14.75	17.6	6.78	2.538
02/08/2005	3	0.0	14.5	1897.84	0.0	0.16	0.00	0.16	106.69	16.9	18.2	2.52	298.3	810.4	1.1	34.5	0.2	9.62	12.89	18.1	6.82	1.775
02/08/2005	4	4.1	19.9	5573.46	0.0	0.16	0.00	0.16	181.47	20.0	46.7	0.43	64.8	137.4	0.6	9.1	0.3	9.51	3.79	17	7.2	1.907
02/08/2005	5	5.2	19.1	4606.24	15.5	0.08	3.62	19.21	218.86	30.7	26.1	1.49	203.6	436.9	0.5	17.1	0.2	9.45	1.37	16.7	7.58	2.618
02/08/2005	6	4.0	28.7	4965.61	7.0	0.57	0.00	7.54	448.73	16.0	25.0	1.17	259.0	323.3	1.7	24.1	0.2	8.69	22.36	18.2	6.77	0.812
02/08/2005	7	5.9	22.0	4138.54	0.0	0.32	0.00	0.32	168.60	10.3	5.3	1.70	235.2	533.4	1.4	43.0	0.3	9.88	12.25	18.1	6.79	3.042
02/08/2005	8	0.0	18.8	3424.94	6.5	0.03	0.00	6.52	79.18	14.0	42.9	1.78	255.9	548.6	3.7	49.0	0.3	10.64	15.3	18.5	6.76	0.747
02/08/2005	9	0.9	22.0	3087.09	0.0	0.46	0.00	0.46	238.26	12.0	46.7	1.21	223.2	477.5	1.9	39.7	0.35	10.12	17.01	18.3	6.76	1.333
02/08/2005	10	0.0	17.3	1780.15	0.0	0.08	0.00	0.08	173.01	12.4	58.1	0.95	170.2	377.9	1.0	31.7	0.35	9.13	21	18.8	6.73	1.181
02/08/2005	11	3.8	18.6	2073.08	0.0	0.03	0.00	0.03	201.05	12.8	50.0	0.80	88.4	160.0	0.5	17.8	0.2	9.7	21.5	17.6	6.75	0.773
02/08/2005	12	1.4	27.6	1757.22	0.0	0.46	0.00	0.46	164.36	16.0	25.0	1.17	259.0	323.3	1.7	24.1	0.2	8.69	22.36	18.2	6.77	0.812
2-6/11/2005	1	0.6	28.8	1217.23	0.0	0.16	7.43	7.59	379.56	18.9	17.6	2.86	325.0	543.5	4.5	14.5	0.5	9.61	13.29	22.4	6.9	1.686
2-6/11/2005	2	0.6	36.6	1211.14	0.0	0.19	8.23	8.42	466.86	20.6	37.1	2.02	267.1	323.1	5.8	31.1	0.45	9.93	11.53	23.6	6.94	1.398
2-6/11/2005	3	2.2	39.6	1365.79	0.0	0.08	9.54	9.63	597.00	27.0	24.4	0.84	79.0	137.4	6.1	15.6	0.4	9.08	11.12	21.9	6.94	1.242
2-6/11/2005	4	3.4	32.4	2380.51	0.0	0.30	11.74	12.03	482.05	9.5	85.7	3.41	272.0	752.1	4.8	19.6	0.55	8.73	6.45	21.5	7.21	2.087
2-6/11/2005	5	0.4	33.6	2247.85	1.6	0.40	8.39	10.41	553.24	14.0	47.6	0.78	93.0	261.5	5.4	21.0	0.4	8.56	7.07	20.9	7.17	1.626
2-6/11/2005	6	1.1	32.6	1794.66	0.0	0.52	17.25	17.87	594.98	30.0	45.2	3.93	309.6	811.0	8.2	40.2	0.5	9.23	7.07	21.2	7.16	1.795
2-6/11/2005	7	0.0	20.3	1215.82	0.0	0.00	9.63	9.63	964.08	6.3	50.0	2.20	209.0	2962.6	2.3	49.7	0.65	10.05	11.9	21.3	6.96	0.856
2-6/11/2005	8	0.0	17.6	1093.92	0.0	0.22	14.04	14.26	737.80	7.4	95.5	2.46	241.4	464.4	1.3	61.7	0.6	10.75	13.21	21.3	6.92	0.514
2-6/11/2005	9	0.0	10.4	783.68	0.0	0.00	9.63	9.63	792.67	6.0	35.3	1.34	160.3	178.7	0.6	40.4	0.65	10.31	13.3	21.2	6.92	0.670
2-6/11/2005	10	0.3	20.0	1150.54	0.0	0.11	11.56	11.66	663.43	9.7	75.9	1.13	200.4	278.9	1.4	25.6	0.6	10.16	13.26	21	6.93	0.604
2-6/11/2005	11	1.7	38.0	1433.64	5.3	0.22	9.78	15.32	649.83	14.4	88.9	0.79	88.9	176.9	2.5	17.7	0.3	9.16	11.59	18.7	6.94	0.992
2-6/11/2005	12	4.7	27.5	1358.07	4.8	0.65	7.96	13.45	853.81	14.0	64.3	0.59	81.4	137.0	2.4	19.4	0.4	8.81	13.27	20.9	6.95	0.951
09/02/2006	1	7.0	28.1	2792.06	5.5	0.00	20.73	26.27	772.16	23.5	25.8	1.42	115.5	472.4	3.6	32.8	0.35	8.13	15.79	23.4	7.3	1.645
09/02/2006	2	7.5	29.8	2260.72	11.0	0.00	21.81	32.77	599.13	29.3	13.6	1.91	195.1	500.2	3.6	53.4	0.35	7.95	16.72	26	7.28	1.637
09/02/2006	3	8.9	37.4	2898.75	8.3	0.00	18.39	26.70	649.73	28.0	14.3	0.84	46.0	166.4	4.3	11.7	0.3	7.66	16.98	25.5	7.31	1.280
09/02/2006	4	1.3	24.9	3169.21	3.0	0.00	21.07	24.04	704.92	30.7	21.7	1.33	78.7	356.3	4.8	17.7	0.4	7.78	12.88	25	7.39	1.622
09/02/2006	5	0.5	28.0	2910.45	2.7	0.00	20.87	23.55	677.02	30.0	16.7	2.71	148.6	388.9	8.4	68.3	0.4	7.62	13.66	26	7.47	2.348
09/02/2006	6	6.7	38.5	4020.15	3.3	0.00	26.98	30.30	1070.63	32.0	15.6	2.48	160.7	498.1	11.8	39.9	0.35	7.62	13.86	25.1	7.41	1.275
09/02/2006	7	6.5	32.1	2957.94	0.8	0.00	20.88	21.63	863.25	15.5	6.5	1.40	142.2	339.1	2.8	42.0	0.45	9.13	17.8	25.5	7.34	

Laguna Garzón																										
Fecha	Estación	PO4 ug/l	PT ug/l	SI ug/l	NH4 ug/l	NO2 ug/l	NO3 ug/l	NID ug/l	NT ug/l	SS mg/l	%MOS	%Mosed	PTsed ug/gP	NTsed ug/gP	Cl a fito ug/l	Cl a fitobento	Z m	OD m/l	KmSlcm	T °C	pH	KD m				
15/02/2005	1	23	59.3	2888.0	10.9	2.0	0.0	12.8	217.6	53.0	34.0	3.5	164.2	74.0	19.1	34.2	0.4	9.2	20.9	26.1	8.3	1.0				
15/02/2005	2	25.5	71.4	3140.6	12.7	1.1	0.0	13.8	393.6	52.0	21.2	13.3	618.9	369.4	0.0	126.7	0.4	8.1	20.3	25.9	8.3	0.7				
15/02/2005	3	22.5	54.3	1171.5	14.3	0.7	0.0	15.0	53.9	69.5	22.5	3.2	169.8	85.8	14.5	155.6	0.4	9.7	20.4	26.3	8.3	4.9				
15/02/2005	4	14.4	22.1	3225.6	19.6	0.6	0.0	20.2	24.5	10.5	19.0	3.7	231.9	167.0	5.1	33.2	0.5	6.5	11.2	21.6	8.4	3.6				
15/02/2005	5	15.5	27.2	3075.8	19.1	0.7	0.0	19.8	31.7	20.7	35.5	8.1	445.6	264.5	6.5	115.4	0.5	7.1	11.6	22.0	8.4	2.0				
15/02/2005	6	18.5	32.6	3726.1	21.0	1.3	0.0	22.3	16.3	26.9	25.0	10.8	562.5	295.3	3.9	124.2	0.5	7.5	10.9	21.7	8.5	1.5				
15/02/2005	7	12.8	12.8	1156.5	12.7	0.3	0.0	13.0	0.0	5.7	15.0	1.5	115.3	35.7	1.0	23.1	0.4	7.9	19.7	22.4	8.2	0.7				
15/02/2005	8	13.7	17.4	881.7	19.2	0.2	0.0	19.4	0.0	17.5	0.0	1.4	110.9	31.1	1.4	19.3	0.4	8.5	19.6	24.3	8.3	3.0				
15/02/2005	9	18.1	24.0	2326.9	16.7	0.2	0.0	16.9	153.0	18.0	17.8	1.6	126.6	50.2	2.2	16.6	0.5	8.5	19.5	24.0	8.3	1.8				
15/02/2005	10	16.6	16.6	1712.5	15.4	0.0	0.0	15.5	84.3	9.7	13.8	0.9	63.4	10.8	1.9	14.8	0.4	8.6	23.3	25.8	8.4	0.5				
15/02/2005	11	14.6	14.6	1248.4	13.1	0.7	0.0	13.8	0.0	6.9	54.2	1.4	116.6	30.2	1.7	15.1	0.5	8.9	23.2	27.9	8.3	1.3				
03/05/2005	12	16.0	18.3	1292.7	15.2	0.7	0.0	15.9	0.0	7.4	15.4	0.7	51.7	10.5	1.7	10.7	0.6	8.9	23.8	26.0	8.3	0.9				
03/05/2005	1	21.1	54.3	3343.5	0.0	3.0	0.0	3.0	436.6	59.2	88.1	1.2	94.3	71.3	15.5	10.1	0.3	11.3	17.2	20.7	7.3	3.0				
03/05/2005	2	20.1	64.8	3088.2	0.0	1.7	0.0	1.7	347.8	45.1	97.6	5.6	187.1	124.2	18.6	9.4	0.3	11.6	17.2	20.6	7.3	2.0				
03/05/2005	3	16.8	49.7	2942.0	0.0	1.3	0.0	1.3	576.4	32.0	92.8	1.2	140.3	323.1	15.3	27.5	0.5	12.1	17.7	20.2	7.3	2.6				
03/05/2005	4	27.8	57.4	5686.2	0.0	2.7	0.0	2.7	511.8	52.9	78.4	8.8	198.6	89.1	6.8	27.1	0.2	9.6	1.7	16.4	8.1	11.4				
03/05/2005	5	18.4	56.2	3307.7	0.0	1.7	0.0	1.7	365.6	50.0	80.0	9.6	356.8	672.0	10.1	55.1	0.1	9.8	2.0	22.2	8.2	5.6				
03/05/2005	6	32.7	89.3	6260.2	0.0	3.4	0.0	3.4	621.8	57.1	70.0	6.9	296.0	723.1	6.0	36.0	0.3	9.6	1.7	17.3	8.2	8.5				
03/05/2005	7	13.4	19.9	4624.2	26.6	1.5	0.0	28.1	144.1	14.2	14.2	0.5	51.7	59.2	1.8	11.2	0.3	11.3	10.0	20.1	7.4	1.4				
03/05/2005	8	23.4	29.0	4218.0	31.0	2.0	0.0	33.0	344.7	23.0	23.0	0.6	72.0	62.2	2.5	11.4	0.4	10.9	11.1	19.3	7.4	1.3				
03/05/2005	9	12.4	15.8	3351.4	40.7	1.0	0.0	41.7	292.4	13.0	47.1	1.0	81.4	77.2	0.4	15.9	0.4	10.5	13.3	18.8	7.5	1.0				
03/05/2005	10	23.3	55.8	3490.6	9.5	3.0	0.0	12.5	327.6	61.3	38.8	1.5	68.4	59.3	3.1	14.2	0.3	10.8	13.5	18.7	7.4	4.4				
03/05/2005	11	19.3	47.7	3464.3	12.9	2.3	0.0	15.2	441.8	40.0	25.0	10.5	279.5	457.8	2.1	19.8	0.8	10.5	13.4	19.3	7.4	4.8				
03/05/2005	12	21.3	80.3	2783.2	0.9	0.8	0.0	1.7	560.3	108.6	21.1	1.5	57.1	30.7	9.2	12.5	0.3	10.7	14.1	22.3	7.4	4.7				
01/08/2005	1	14.3	43.5	3872.2	36.1	1.4	21.9	59.4	303.0	25.0	20.0	1.7	153.7	443.5	1.2	9.3	1.4	9.8	2.8	14.9	6.9	3.2				
01/08/2005	2	0.0	25.9	3995.1	0.0	1.9	8.6	10.5	309.6	30.0	41.7	6.2	316.2	1411.6	11.0	13.0	1.6	9.3	2.8	15.4	6.8	2.7				
01/08/2005	3	0.8	22.2	3721.4	0.0	1.8	22.0	23.8	233.9	32.9	43.5	9.0	494.9	1856.7	13.3	39.2	1.8	9.4	2.8	15.3	6.9	2.7				
01/08/2005	4	2.0	33.7	3824.1	9.5	1.4	24.0	34.9	306.8	36.9	41.7	2.2	153.7	586.6	7.4	22.4	1.7	8.7	1.9	14.9	6.9	2.7				
01/08/2005	5	1.3	24.5	4049.2	2.9	1.3	41.2	45.4	123.5	40.0	45.8	1.2	95.2	317.3	8.3	14.3	1.5	8.8	1.8	15.2	6.9	2.6				
01/08/2005	6	1.1	31.8	2476.4	5.0	1.1	19.5	22.6	193.2	27.3	33.3	2.0	150.4	513.0	6.6	15.9	1.6	8.6	1.8	15.0	6.9	2.4				
01/08/2005	7	3.8	27.5	3684.6	36.2	1.2	38.3	75.6	253.3	23.6	69.2	0.4	46.4	82.8	5.0	6.3	1.8	9.3	2.7	14.4	6.8	2.5				
01/08/2005	8	6.6	29.2	3130.1	39.5	1.4	41.7	82.6	246.8	34.5	31.6	0.9	77.8	233.8	2.5	5.5	1.7	9.2	2.7	14.4	6.8	2.4				
01/08/2005	9	0.7	41.7	2978.3	22.6	1.0	25.5	49.0	141.1	172.7	23.2	0.7	103.5	208.6	6.7	9.1	1.7	9.1	2.9	14.7	6.8	2.3				
01/08/2005	10	0.0	31.8	3067.2	5.9	1.1	14.9	21.9	190.2	25.5	21.4	0.9	80.9	177.3	8.5	5.3	1.8	9.6	2.8	15.8	6.8	2.9				
01/08/2005	11	5.4	37.8	2711.6	23.5	0.9	26.3	50.6	180.6	23.6	30.8	11.0	681.1	2194.2	5.1	50.2	2.4	9.4	2.6	15.7	6.8	3.4				
01/08/2005	12	5.0	44.0	3516.4	23.7	1.2	21.9	48.8	327.9	36.4	10.0	1.0	95.7	268.8	3.0	8.8	1.8	9.7	2.7	15.9	6.8	3.5				
2-6/11/2005	1	8.2	86.7	1327.2	0.0	0.4	9.8	10.2	835.3	113.3	17.6	0.9	69.5	161.2	22.0	10.6	0.3	9.1	20.1	20.3	6.7	2.0				
2-6/11/2005	2	4.4	42.8	1152.2	0.0	0.5	12.1	12.6	709.2	45.6	19.5	0.9	76.3	43.9	5.3	9.9	0.4	8.6	21.1	20.4	6.7	2.2				
2-6/11/2005	3	6.1	75.1	1188.9	0.0	0.2	10.0	10.2	488.6	87.1	27.9	1.1	65.9	144.6	6.4	20.2	0.3	8.9	20.9	20.6	6.7	2.1				
2-6/11/2005	4	5.7	46.7	2471.5	0.0	0.4	10.5	10.9	805.8	24.6	31.3	10.4	547.4	1257.8	4.9	128.1	0.6	8.5	6.8	19.8	7.1	2.6				
2-6/11/2005	5	5.8	42.0	2896.9	0.0	0.9	11.7	12.7	763.0	21.1	37.5	4.2	350.3	872.8	4.3	56.0	0.4	8.4	5.5	20.2	7.2	1.7				
2-6/11/2005	6	5.9	44.3	2192.2	0.0	0.9	11.0	11.9	518.8	41.1	37.8	2.7	200.0	245.8	5.1	18.1	0.6	8.6	7.4	19.7	7.1	2.8				
2-6/11/2005	7	7.2	67.3	1476.5	0.0	1.1	12.3	13.3	705.4	75.7	13.2	0.9	81.0	68.9	5.5	14.2	0.6	9.0	20.5	20.3	6.7	4.2				
2-6/11/2005	8	6.9	59.8	1306.8	0.0	0.2	8.9	9.1	638.7	57.1	27.5	1.3	82.1	201.8	3.6	15.0	0.5	8.8	20.3	20.5	6.7	2.4				
2-6/11/2005	9	3.3	31.3	1179.1	0.0	0.3	11.2	11.5	606.1	30.0	50.0	1.3	77.9	227.8	2.6	12.5	0.6	8.0	18.1	20.1	6.8	1.9				
2-6/11/2005	10	14.2	115.1	903.7	13.8	0.6	10.9	25.3	807.2	188.3	23.0	1.4	30.0	188.1	6.1	15.3	0.7	8.5	19.7	20.2	6.7	2.2				
2-6/11/2005	11	12.8	90.8	933.9	4.4	0.5	3.6	8.6	514.0	87.1	23.0	13.5	279.3	267.8	7.0	135.1	1.0	9.4	20.1	19.8	6.7	3.7				
2-6/11/2005	12	6.4	49.4	1125.5	7.0	0.2	5.4	12.5	742.6	29.9	40.5	1.9	53.2	78.4	9.0	0.8	9.0	23.1	20.1	6.7	2.2					
10/02/2006	1	2.4	12.0	1329.8	0.0	0.0	21.5	21.5	692.3	29.0	3.4	7.4	356.4	1085.5	1.7	88.7	0.5	7.5	27.9	25.7	7.5	0.7				
10/02/2006	2	8.3	31.5	1319.5	0.0	0.0	20.2	20.2	551.5	47.0	23.4	2.1	115.6	296.2	6.6	61.4	0.4	8.4	28.9	25.3	7.5	1.3				
10/02/2006	3	5.1	8.2	1320.4	0.0	0.0	24.0	24.0	409.5	26.0	19.2	2.6	139.5	379.3	1.4	52.9	0.5	7.0	27.4	25.5	7.6	0.3				
10/02/2006	4	2.5	2.5	1024.2	0.0	0.0	23.0	23.0	223.2	17.0	17.6	7.1	294.8	818.0	1.6	36.0	0.6	8.7	18.2	25.5	7.7	0.9				
10/02/2006	5	2.7	13.6	1403.3	0.0	0.1	22.3	22.4	500.0	26.0	25.0	2.1	100.2	452.7	3.9	59.0	0.4	8.9	20.9	24.6	7.7	1.5				
10/02/2006	6	3.0	11.2	1552.3	0.0	0.0	21.4	21.4	473.1	22.5	14.8	1.2	86.1	377.4	13.0	0.5	9.7	17.7	26.0	7.8	0.6					
10/02/2006	7	2.9	5.0	788.1	455.4	0.0	21.4	476.7	372.2	20.8	24.0	2.1	119.2	541.2	1.2	22.3	0.4	8.6	26.4	24.4	7.7	1.2				
10/02/2006	8	3.6	7.0	889.2	0.0	0.0	21.0	21.0	342.8	14.0	21.4	1.2	147.9	676.3	3.1	23.5	0.5	6.3	26.8	22.9	7.7	1.2				
10/02/2006	9	5.3	24.4	998.2	0.0	0.0	20.7	20.7	627.7	25.5	11.8	1.2	86.8	327.7	1.8	10.5	0.5	7.2	27.0	24.5	7.7	1.0				
10/02/2006	10	28.0	95.9																							

Laguna de Rocha																						
Fecha	Estación	PO4 ug/l	PT ug/l	Si ug/l	NH4 ug/l	NO2 ug/l	NO3 ug/l	NID ug/l	NT ug/l	SS mg/l	%Moss	%Mosed	PTsed ug/gP	NTsed ug/gP	Cla fito ug/l	Cla fitobento	Z m	OD mg/l	K mSc/m	T °C	pH	KD m
13/02/2005	1	25.4	69.0	3325.7	3.7	2.4	0.0	6.1	182.7	77.8	1.2	0.8	96.0	23.3	29.9	9.4	0.8	8.6	10.0	23.7	7.7	9.4
13/02/2005	2	28.6	78.5	3607.2	4.5	2.7	0.0	7.2	167.7	120.0	1.1	0.7	128.1	42.7	14.7	13.3	1.1	8.4	10.1	23.9	7.7	6.3
13/02/2005	3	32.6	85.5	3303.7	43.8	3.8	0.0	3.7	481.4	15.0	91.7	6.7	155.1	57.3	7.9	2.7	0.9	8.0	10.7	24.4	7.6	8.7
13/02/2005	4	21.5	44.6	3043.6	0.0	2.9	0.0	2.9	243.6	56.0	23.2	2.6	237.3	257.3	9.7	1.6	0.9	9.1	9.3	22.6	7.7	3.9
13/02/2005	5	33.8	90.3	3233.2	0.0	2.6	0.0	2.6	185.5	90.0	40.0	0.6	179.5	52.3	23.2	1.6	0.9	8.3	9.8	23.2	7.7	7.9
13/02/2005	6	26.6	70.1	2903.8	0.0	2.6	0.0	2.6	192.0	77.1	25.9	0.6	89.2	15.9	20.1	0.6	0.8	8.4	9.7	23.4	7.7	7.6
13/02/2005	7	30.5	73.3	3018.8	0.0	2.7	0.0	2.7	238.8	57.0	26.3	0.9	116.1	52.3	17.9	0.9	0.8	8.2	10.0	25.6	7.6	5.7
13/02/2005	8	25.3	55.9	3078.0	0.0	2.2	0.0	2.2	99.0	92.0	31.6	1.2	133.9	99.6	7.3	0.5	0.0	8.7	10.0	25.7	7.6	2.8
13/02/2005	9	19.4	19.4	3325.7	3.3	2.8	0.0	3.2	275.0	54.0	11.0	3.2	52.9	10.1	27.3	2.3	0.9	8.4	9.8	25.0	7.7	7.4
13/02/2005	10	27.5	61.9	3232.2	8.2	2.6	0.0	10.7	115.1	50.0	18.0	1.7	192.7	116.6	10.2	3.0	1.0	8.9	9.8	24.4	7.7	4.3
13/02/2005	11	19.5	40.7	3107.4	0.0	2.9	0.0	2.9	58.0	19.8	15.4	1.5	160.1	30.7	4.2	1.7	0.8	8.8	9.9	26.4	7.7	1.8
13/02/2005	12	30.1	58.5	3499.7	0.0	2.8	0.0	2.8	42.0	38.0	21.1	1.6	197.7	138.7	2.5	0.6	1.3	8.4	10.0	25.4	7.7	3.3
29/04/2005	1	24.2	36.9	1879.1	2.8	2.7	0.0	5.5	539.5	12.1	75.0	2.4	160.2	141.3	2.2	24.1	0.4	10.5	8.5	20.1	6.8	2.5
29/04/2005	2	23.5	38.8	1941.8	0.0	3.7	0.0	3.7	481.4	15.0	91.7	6.7	302.2	248.5	2.9	46.2	0.5	12.0	10.1	18.4	6.7	3.2
29/04/2005	3	22.8	35.3	1918.3	0.0	2.1	0.0	8.1	372.0	16.3	84.6	1.7	164.8	206.1	0.7	38.4	0.4	11.2	9.5	19.0	6.8	2.3
29/04/2005	4	30.5	37.4	4559.0	0.0	1.7	0.0	1.7	128.4	26.3	52.4	3.9	200.9	276.6	0.3	48.5	0.5	11.1	6.6	18.8	6.9	2.7
29/04/2005	5	43.3	56.3	3077.3	26.0	1.8	0.0	27.8	416.5	12.5	50.0	1.2	113.3	92.1	0.7	26.4	0.6	11.0	9.3	18.4	6.8	2.1
29/04/2005	6	44.4	62.8	3082.7	26.8	2.6	0.0	29.4	380.2	18.6	51.2	1.7	156.5	204.8	1.1	17.3	0.5	11.3	6.8	18.1	6.9	3.3
29/04/2005	7	26.7	29.5	2431.6	0.0	1.9	0.0	1.9	64.5	10.4	10.0	1.0	105.1	88.1	5.1	18.8	0.5	12.2	12.5	16.9	6.7	1.4
29/04/2005	8	24.8	25.6	2311.3	0.0	1.6	0.0	1.6	155.4	7.0	0.9	0.9	100.6	164.3	2.3	12.1	0.4	10.0	14.0	18.7	6.7	0.6
29/04/2005	9	18.5	19.6	1253.4	0.0	1.6	0.0	1.6	90.8	16.6	16.0	0.9	0.0	0.0	4.2	25.4	0.5	12.1	15.2	17.5	6.7	1.3
29/04/2005	10	18.3	23.2	797.5	0.0	1.2	0.0	1.2	0.0	11.3	12.0	1.3	106.1	25.6	7.3	17.1	0.6	11.6	16.8	15.9	6.7	1.6
29/04/2005	11	15.5	15.5	700.7	0.0	1.1	0.0	1.1	0.0	2.5	2.0	0.7	104.0	167.3	2.8	13.2	0.5	10.3	19.3	15.2	6.7	0.7
29/04/2005	12	19.1	19.1	2315.5	0.0	2.1	0.0	2.1	2.0	8.1	1.0	0.4	48.1	42.4	6.0	2.9	0.7	9.4	15.1	14.5	6.9	1.5
30/07/2005	1	6.3	55.5	944.8	0.0	0.2	0.0	0.2	217.3	78.2	16.3	1.2	109.3	210.2	19.8	26.0	0.3	9.7	19.7	18.0	7.3	7.8
30/07/2005	2	13.6	80.7	761.5	0.0	0.2	0.0	0.2	442.9	18.0	3.1	1.2	189.0	427.8	21.3	27.1	0.3	9.3	15.9	17.4	7.4	4.9
30/07/2005	3	5.5	70.5	143.3	0.0	0.0	0.0	0.0	241.8	156.4	16.3	1.2	157.2	247.2	22.8	24.2	0.3	9.9	22.0	18.1	7.3	11.8
30/07/2005	4	0.0	33.2	671.6	0.0	0.0	0.0	0.0	305.3	14.4	21.7	1.4	175.4	270.4	2.3	33.8	0.4	9.1	22.4	15.1	7.3	1.3
30/07/2005	5	6.7	29.2	876.6	0.0	0.1	0.0	0.1	221.2	11.5	39.1	1.5	211.6	284.3	1.8	29.6	0.4	8.7	23.7	15.4	7.3	1.7
30/07/2005	6	4.0	47.5	854.6	0.0	0.0	0.0	0.0	372.0	20.4	24.2	0.9	100.3	117.5	4.0	15.1	0.4	9.0	21.2	15.6	7.3	1.2
30/07/2005	7	0.0	29.3	97.5	0.0	0.0	0.0	0.0	219.7	12.8	21.9	1.3	97.3	156.6	1.9	13.3	0.3	10.3	21.8	17.4	7.3	1.1
30/07/2005	8	0.0	35.4	227.3	0.0	0.0	0.0	0.0	176.0	19.2	12.0	3.0	113.8	210.3	1.9	6.9	0.3	9.7	22.2	18.2	7.3	1.6
30/07/2005	9	10.7	109.5	661.3	0.0	0.1	1.2	1.3	477.1	27.6	43.8	1.2	141.1	251.5	1.9	12.4	0.4	8.8	23.0	17.1	7.3	10.5
30/07/2005	10	4.7	46.5	172.6	0.0	0.0	0.0	0.0	236.7	19.5	28.2	0.9	85.9	225.4	1.8	10.8	0.3	9.3	23.2	17.9	7.3	1.1
30/07/2005	11	4.5	34.0	68.2	0.0	0.1	0.0	0.1	200.5	17.5	22.9	1.4	78.6	195.6	2.5	9.3	0.3	9.7	22.9	18.5	7.3	2.0
30/07/2005	12	10.4	54.4	671.8	0.0	0.2	0.0	0.2	135.1	31.8	21.4	0.2	65.2	20.4	1.2	10.0	0.3	8.7	26.3	16.6	7.2	2.3
2-6/11/2005	1	5.4	77.4	704.0	0.0	0.4	9.5	9.9	394.8	141.4	19.2	1.5	58.6	16.9	5.5	18.9	0.4	8.3	24.2	24.6	7.5	5.8
2-6/11/2005	2	6.7	87.3	837.0	0.0	0.5	9.7	45.2	420.8	18.7	22.0	3.1	185.0	318.7	3.9	24.4	0.3	9.9	24.4	24.6	7.5	34.9
2-6/11/2005	3	5.8	59.3	921.5	0.0	0.4	9.1	9.5	463.2	83.3	24.0	5.2	185.0	314.4	4.8	43.0	0.4	8.3	24.9	26.9	7.5	5.3
2-6/11/2005	4	11.6	75.6	1551.8	0.0	0.2	11.7	11.9	430.4	90.0	24.1	4.2	315.0	327.5	5.7	63.1	0.5	7.7	16.0	25.9	7.7	4.2
2-6/11/2005	5	2.1	38.4	622.5	0.0	0.3	8.4	8.7	463.9	57.8	30.5	2.2	238.5	289.5	1.1	29.0	0.5	8.5	25.6	24.5	7.5	2.1
2-6/11/2005	6	7.1	84.1	872.6	29.6	1.1	10.1	40.8	496.8	141.4	29.3	1.4	51.9	224.6	6.9	16.1	0.4	6.8	27.5	27.1	7.5	8.4
2-6/11/2005	7	1.5	19.7	361.6	0.0	0.2	8.9	9.1	818.5	15.2	37.5	0.6	57.7	56.6	0.4	8.3	0.4	9.7	27.5	24.1	7.5	0.5
2-6/11/2005	8	2.6	18.1	788.1	0.0	0.1	13.1	13.2	427.4	17.6	11.8	1.2	41.4	63.0	0.6	16.7	0.3	10.2	29.2	24.3	7.5	0.7
2-6/11/2005	9	4.0	77.8	367.5	0.0	0.4	9.6	10.0	293.9	45.7	17.5	1.0	63.6	39.1	1.0	12.5	0.3	8.6	29.4	25.2	7.5	2.1
2-6/11/2005	10	7.5	22.6	712.3	0.0	0.6	10.1	10.6	424.9	9.2	30.8	0.8	57.7	49.8	0.7	10.9	0.6	8.7	26.8	21.6	7.5	0.6
2-6/11/2005	11	10.7	22.4	605.4	0.0	0.7	10.4	11.1	624.4	11.7	24.2	1.3	144.1	292.1	4.0	8.9	0.4	8.7	28.5	23.0	7.5	1.0
2-6/11/2005	12	5.1	26.2	619.2	29.0	0.3	8.1	37.4	482.0	15.2	23.3	1.6	199.1	206.7	0.4	10.7	0.7	10.2	28.8	20.6	7.5	1.7
06/02/2006	1	29.4	56.2	2970.9	0.0	0.0	19.1	19.1	863.9	89.0	10.2	1.8	147.8	478.1	0.4	8.7	0.1	9.1	48.9	18.8	7.6	5.7
06/02/2006	2	28.0	47.5	3738.2	0.0	0.0	23.4	23.4	882.2	73.8	13.5	2.3	178.2	457.8	0.3	11.5	0.1	9.3	51.5	18.9	7.7	5.7
06/02/2006	3	18.5	39.6	2680.7	0.0	0.0	22.4	22.4	625.0	103.8	16.9	1.9	145.4	89.4	1.4	13.1	0.1	9.1	49.8	18.9	7.6	5.7
06/02/2006	4	31.6	32.8	1169.0	0.0	1.7	24.9	26.7	352.7	45.6	17.1	1.6	163.1	442.9	2.7	26.2	0.3	10.2	35.8	17.4	7.4	1.5
06/02/2006	5	18.9	95.7	1807.1	0.0	0.0	22.1	22.1	894.8	158.1	10.2	1.3	149.4	369.9	10.4	21.0	0.3	10.5	36.0	17.2	7.4	4.8
06/02/2006	6	19.7	53.5	902.1	0.7	0.0	27.3	28.0	402.9	100.0	5.0	1.0	87.0	237.1	1.6	9.0	0.4	10.1	38.9	17.6	7.4	3.3
06/02/2006	7	10.0	104.8	1109.4	3.3	0.0	30.3	33.5	859.0	203.3	11.5	0.6	51.7	195.8	3.5	3.4	0.3	10.8	39.2	18.2	7.4	7.7
06/02/2006	8	15.9	95.4	905.3	0.0	0.5	23.9	24.4	844.3	187.3	7.8	1.2	171.8	220.0	10.2	8.6	0.3	9.1	11.8	18.2	7.4	3.0
06/02/2006	9	19.7	55.1	948.9	0.0	0.1	23.5	23.6	428.8	111.7	7.5	2.0	188.2	265.4	6.1	18.8	0.4	10.4	37.2	19.5	7.4	2.5
06/02/2006	10	19.5	31.6	272.5	0.0	0.7	24.7	25.4	264.4	103.3	9.7	0.9	69.3	112.4	2.4	6.7	0.4	1				

Laguna de Castillos

Fecha	Estación	PO4 ug/l	PT ug/l	Si ug/l	NH4 ug/l	NO2 ug/l	NO3 ug/l	NID ug/l	NT ug/l	SS mg/l	%MOss	%MOsed	PTsed ug/gP	NTsed ug/gP	Cla cito ug/l	Cla fitobento	Z m	OD mg/l	K ms/cm	T °C	pH	KD m
14/02/2005	1	25.0	62.4	4367.2	30.7	2.4	0.0	33.1	0.0	42.0	19.0	0.9	100.1	81.5	3.2	45.0	0.9	8.0	9.5	24.5	7.4	3.5
14/02/2005	2	22.9	22.9	4068.7	0.0	2.4	0.0	2.4	0.0	6.0	6.7	0.9	125.8	24.1	2.3	19.9	0.9	8.4	9.0	24.2	7.4	0.9
14/02/2005	3	21.0	21.2	3995.6	0.0	2.5	0.0	2.5	0.0	5.2	13.3	0.6	79.6	51.5	0.8	17.6	0.8	8.2	8.3	24.2	7.5	0.8
14/02/2005	4	26.4	26.4	4097.0	0.0	2.6	0.0	2.6	20.8	27.9	33.3	2.1	244.9	68.0	2.1	6.5	1.0	8.0	10.9	23.1	7.5	2.0
14/02/2005	5	20.7	20.7	3466.9	11.6	1.5	0.0	13.1	0.0	24.7	16.2	2.2	229.1	222.8	3.5	7.9	0.9	7.8	11.5	23.1	7.5	2.0
14/02/2005	6	23.0	23.0	3606.0	0.0	1.7	0.0	1.7	40.3	22.7	35.3	1.9	232.1	103.9	3.2	7.5	1.0	7.8	11.2	23.3	7.5	3.1
14/02/2005	7	16.8	16.8	3381.5	0.0	1.2	0.0	1.2	0.0	4.0	26.4	1.4	187.9	44.4	1.9	39.2	0.7	9.2	13.0	24.5	7.5	1.0
14/02/2005	8	19.0	27.3	3975.5	0.0	2.4	0.0	2.4	453.7	9.6	8.3	1.2	166.1	49.9	1.3	26.0	0.5	8.4	14.0	24.7	7.6	2.7
14/02/2005	9	14.4	14.4	2499.9	0.0	1.3	0.0	1.3	0.0	11.1	44.4	1.2	199.8	26.2	1.7	19.1	0.4	8.3	14.2	25.4	7.6	1.9
01/05/2005	1	47.3	74.1	2185.6	0.0	5.7	0.0	5.7	465.0	8.6	1.0	79.6	69.6	15.5	1.7	9.3	1.8	17.7	6.8	17.7	6.8	3.7
01/05/2005	2	52.7	82.5	2087.0	6.0	4.6	0.0	10.6	562.7	10.0	33.3	2.5	194.8	137.8	2.2	69.7	1.6	9.4	1.4	17.0	6.9	3.8
01/05/2005	3	38.0	63.7	1272.3	0.0	3.8	0.0	3.8	458.8	16.0	0.3	49.0	45.5	11.3	34.1	1.5	8.2	1.8	16.3	6.8	3.8	
01/05/2005	4	21.2	31.0	1913.3	0.0	2.0	0.0	2.0	334.8	15.0	100.0	1.8	120.8	187.5	1.8	13.5	1.6	10.3	5.0	15.8	6.6	2.4
01/05/2005	5	20.5	40.0	2301.8	0.0	2.0	0.0	2.0	318.1	1.7	0.0	1.8	128.7	244.8	2.0	4.1	1.6	10.5	4.9	16.1	6.7	4.1
01/05/2005	6	21.4	31.6	2342.3	0.0	1.6	0.0	1.6	234.0	0.0	1.6	104.4	97.5	6.4	4.3	1.6	10.4	5.0	15.7	6.7	2.4	
01/05/2005	7	41.4	62.7	3180.3	0.0	3.0	0.0	3.0	539.5	3.3	0.0	1.0	90.7	109.2	3.2	13.1	1.3	10.6	7.8	17.0	6.7	2.4
01/05/2005	8	34.1	45.9	2944.9	0.0	2.2	0.0	2.2	330.0	4.3	66.7	0.6	98.5	93.5	3.5	11.6	1.2	10.9	4.9	17.2	6.7	2.4
01/05/2005	9	28.7	36.8	1930.6	0.0	1.6	0.0	1.6	609.9	2.9	1.0	99.1	103.2	5.2	18.5	1.1	10.6	4.9	17.7	6.7	2.7	
31/07/2005	1	25.1	87.6	1983.5	0.0	1.3	28.6	28.6	130.6	60.0	10.4	1.4	187.4	388.7	2.3	5.0	1.6	8.9	0.4	17.0	7.4	5.3
31/07/2005	2	16.6	68.6	2984.6	0.0	1.4	5.7	5.7	93.7	32.0	29.2	2.7	246.3	752.3	2.4	17.3	1.5	8.9	0.1	15.9	7.6	4.0
31/07/2005	3	15.5	65.1	2158.9	0.0	1.5	6.8	6.8	177.1	28.0	19.0	0.8	209.9	187.5	1.0	13.2	1.4	8.7	0.1	14.4	7.5	3.5
31/07/2005	4	23.7	65.9	2007.8	0.0	0.9	30.8	31.8	163.0	29.3	2.3	359.5	623.8	2.0	4.9	1.6	9.4	0.5	16.4	7.2	1.1	
31/07/2005	5	21.1	64.9	2818.5	0.0	2.3	20.5	22.8	148.5	32.2	35.7	1.9	294.8	523.8	0.8	15.8	1.5	9.3	0.4	16.3	7.1	1.5
31/07/2005	6	17.5	58.3	1961.5	0.0	1.0	19.8	20.7	79.6	32.0	50.0	0.7	212.5	392.9	1.0	4.0	1.5	9.2	0.4	16.5	7.2	1.5
31/07/2005	7	38.3	76.7	3851.0	9.9	2.1	34.8	46.8	91.1	52.0	38.5	1.7	164.3	141.4	1.8	3.9	1.3	9.7	0.4	15.7	7.1	0.9
31/07/2005	8	23.4	64.3	3050.1	4.6	0.4	23.0	28.0	593.7	35.0	35.7	1.4	165.4	299.9	1.8	6.1	0.9	9.7	0.4	16.3	7.1	1.3
31/07/2005	9	31.0	76.0	3586.6	0.0	1.4	30.9	32.3	620.5	23.5	15.0	4.4	545.4	1412.5	1.2	12.8	0.9	9.9	0.4	15.9	7.1	1.6
2-6/11/2005	1	37.3	117.9	1937.6	0.0	5.5	64.7	70.2	1620.5	170.0	11.8	2.1	230.1	576.8	15.8	6.0	0.9	9.2	0.4	22.3	7.4	18.3
2-6/11/2005	2	23.8	101.4	1352.9	0.0	1.1	56.5	57.5	1508.7	106.7	20.3	0.7	102.7	303.8	10.6	8.3	1.0	9.0	0.4	22.4	7.3	12.4
2-6/11/2005	3	20.3	98.5	1818.8	0.0	2.2	29.6	31.8	1504.4	94.3	19.7	0.6	49.2	100.5	7.0	11.0	0.7	8.5	0.4	22.8	7.3	7.8
2-6/11/2005	4	39.1	98.9	1791.4	0.0	3.1	95.3	98.5	1662.4	91.4	3.1	1.5	184.1	466.5	2.4	4.3	1.0	9.2	0.6	20.8	7.1	6.9
2-6/11/2005	5	38.9	99.6	1840.0	0.0	2.5	111.3	113.7	1514.1	77.1	7.4	1.9	233.9	483.7	2.0	2.4	0.9	9.0	0.6	20.4	7.1	7.7
2-6/11/2005	6	43.6	110.3	1838.9	0.0	3.6	117.9	121.5	1880.1	103.8	9.6	2.9	251.2	376.1	2.6	2.2	1.0	9.7	0.6	19.7	7.1	6.6
2-6/11/2005	7	43.5	116.1	1762.4	0.0	2.9	124.4	127.3	1639.7	98.6	17.4	0.9	187.8	219.5	2.7	3.9	0.6	7.6	0.5	22.3	7.1	6.0
2-6/11/2005	8	40.7	96.7	1413.1	8.4	3.1	118.5	130.0	1741.8	94.3	22.7	0.7	126.0	91.7	3.9	2.2	0.4	8.7	0.4	22.8	7.1	7.9
2-6/11/2005	9	50.2	133.7	2247.9	0.0	3.5	97.4	100.9	1734.7	204.3	11.2	1.9	156.4	444.9	8.7	4.9	0.3	8.6	0.4	22.9	7.2	11.8
08/02/2006	1	2.2	2.2	412.1	0.0	0.5	21.3	21.8	483.0	8.4	19.0	2.7	183.4	633.2	0.8	27.2	0.8	6.4	15.8	20.1	7.3	0.6
08/02/2006	2	1.3	1.3	499.4	2.8	0.0	23.6	26.4	733.2	8.0	25.0	0.9	116.8	464.5	0.2	16.3	0.8	6.8	15.5	20.1	7.3	0.6
08/02/2006	3	5.7	5.7	474.1	0.0	0.0	22.7	22.7	633.6	6.4	37.5	1.5	145.9	444.1	0.4	58.1	0.6	6.2	15.0	19.8	7.3	0.7
08/02/2006	4	2.0	2.0	1465.2	0.0	0.0	19.8	19.8	499.3	4.4	18.2	1.3	112.7	404.1	0.9	12.1	0.9	7.6	11.7	20.2	7.4	0.7
08/02/2006	5	2.7	2.7	778.0	1.5	0.0	19.2	20.7	281.3	2.0	33.3	1.0	150.1	417.3	0.2	7.8	0.8	8.5	11.6	21.0	7.4	0.5
08/02/2006	6	2.6	2.6	1855.3	0.0	0.0	19.2	19.2	548.1	8.0	31.3	0.4	200.2	320.5	0.3	10.3	0.9	8.7	12.1	20.4	7.4	0.6
08/02/2006	7	2.9	2.9	438.8	8.2	0.0	18.6	24.8	305.7	14.0	26.4	0.5	124.6	252.8	0.7	10.0	0.6	8.5	21.8	20.5	7.2	0.5
08/02/2006	8	4.0	4.0	581.1	3.2	0.0	20.6	23.8	428.7	16.4	12.2	0.9	152.5	219.6	0.8	8.4	0.5	9.1	23.6	19.6	7.2	0.3
08/02/2006	9	14.7	14.7	442.8	0.0	0.0	27.1	27.1	214.0	13.5	18.5	0.4	126.9	125.1	3.1	4.5	0.3	7.0	43.2	21.8	7.1	0.4
20/06/2006	1	8.3	27.8	812.9	7.6	1.2	0.0	8.8	0.0	15.1	62.5	5.6	311.1	847.5	0.8	12.7	1.2	9.1	1.7	13.2	7.7	16.1
20/06/2006	2	6.7	29.2	805.2	0.2	1.1	0.0	1.3	270.7	23.6	30.8	2.0	192.2	390.8	2.6	13.0	1.1	8.7	1.4	13.4	7.6	16.4
20/06/2006	3	7.3	27.9	653.6	0.0	1.6	0.0	1.6	683.2	28.0	42.9	0.4	103.1	175.6	3.5	9.3	1.0	7.8	1.0	13.3	7.3	16.7
20/06/2006	4	6.6	29.2	818.8	201.9	0.7	0.0	202.6	0.0	26.0	30.8	1.6	271.9	542.7	1.4	6.4	1.2	9.2	4.6	14.1	7.3	13.7
20/06/2006	5	4.3	15.2	335.9	17.4	0.8	0.0	18.2	0.0	10.9	33.3	0.8	189.5	246.4	2.8	5.7	1.2	9.4	4.6	14.0	7.4	12.3
20/06/2006	6	3.7	15.1	543.5	15.1	0.4	0.0	15.5	0.0	20.0	40.0	2.0	247.1	454.3	5.2	5.5	1.3	9.6	5.0	13.9	7.4	11.6
20/06/2006	7	3.7	9.5	453.8	7.6	0.4	0.0	8.0	552.3	18.0	11.1	0.3	158.3	262.8	4.0	9.6	1.0	8.6	6.5	13.4	7.4	9.6
20/06/2006	8	2.7	2.7	650.1	13.4	1.2	0.0	14.6	290.2	36.1	18.2	0.4	202.1	405.6	3.1	13.9	0.8	9.8	6.5	13.5	7.5	7.0
20/06/2006	9	4.0	16.1	941.6	0.0	0.2	0.0	0.2	479.1	20.0	20.0	1.3	242.2	755.4	4.5	62.6	0.7	9.9	6.8	13.6	7.4	10.3

Laguna del Diario biomasa de plantas gPS/m2

Muestreo	Riqueza	P. gayi	P. illinoensis	M. quitense	BMTOTAL
09/02/2005	1	15.9	0.0	0.0	15.9
09/02/2005	1	165.0	0.0	0.0	165.0
09/02/2005	3	3.6	266.4	1.8	271.8
09/02/2005	1	200.8	0.0	0.0	200.8
09/02/2005	1	236.6	0.0	0.0	236.6
09/02/2005	1	192.8	0.0	0.0	192.8
02/05/2005	1	161.0	0.0	0.0	161.0
02/05/2005	2	12.5	0.0	1.0	13.5
02/05/2005	1	0.0	176.9	0.0	176.9
02/05/2005	1	105.4	0.0	0.0	105.4
02/05/2005	1	47.7	0.0	0.0	47.7
02/05/2005	1	59.6	0.0	0.0	59.6
02/08/2005	3	0.4	0.0	0.4	0.8
02/08/2005	2	8.9	0.0	0.0	8.9
02/08/2005	2	0.0	86.3	0.0	86.3
02/08/2005	1	3.8	0.0	0.0	3.8
02/08/2005	0	0.0	0.0	0.0	0.0
02/08/2005	1	1.8	0.0	0.0	1.8
2-6/11/2005	2	0.4	103.4	0.0	103.8
2-6/11/2005	1	0.6	0.0	0.0	0.6
2-6/11/2005	1	0.0	175.0	0.0	175.0
2-6/11/2005	1	1.6	0.0	0.0	1.6
2-6/11/2005	0	0.0	0.0	0.0	0.0
2-6/11/2005	1	8.2	0.0	0.0	8.2
09/02/2006	2	0.0	188.9	6.4	195.2
09/02/2006	3	3.0	0.0	83.5	86.5
09/02/2006	1	0.0	141.2	0.0	141.2
09/02/2006	1	0.0	113.3	0.0	113.3
09/02/2006	1	0.0	0.0	37.8	37.8
09/02/2006	2	0.4	0.0	2.4	2.8
20/06/2006	1	0.0	93.4	2.7	96.1
20/06/2006	2	0.9	0.0	153.1	154.0
20/06/2006	1	0.6	105.4	89.5	195.4
20/06/2006	1	0.0	0.0	135.2	135.2
20/06/2006	1	14.9	0.0	105.4	120.2
20/06/2006	1	0.2	0.0	79.5	79.7

Laguna de Castillos biomasa de plantas gPS/m2

Muestreo	Riqueza	R. maritima	Z. palustris	filamentosa	nytea+chara	BM TOTAL
14/02/2005	0	0.0	0.0	0.0	0	0.0
14/02/2005	0	0.0	0.0	0.0	0	0.0
14/02/2005	1	0.0	0.0	0.0	0	0.0
14/02/2005	1	0.0	0.0	0.0	0	0.0
14/02/2005	0	0.0	0.0	0.0	0	0.0
14/02/2005	1	0.0	0.0	0.0	0	0.0
14/02/2005	2	0.0	0.0	0.0	0	0.0
14/02/2005	1	0.4	0.0	0.0	0	0.4
14/02/2005	1	0.0	0.0	0.0	0	0.0
01/05/2005	2	0.0	0.0	1.2	1.2	2.4
01/05/2005	4	1.8	0.2	1.0	0.2	3.2
01/05/2005	5	4.4	13.5	5.0	2.2	25.0
01/05/2005	4	0.0	1.2	0.0	4.0	5.2
01/05/2005	2	0.0	0.0	0.0	1.6	1.6
01/05/2005	2	0.0	0.4	0.4	0.0	0.8
01/05/2005	2	5.6	0.2	0.0	0.0	5.8
01/05/2005	2	1.6	0.0	0.0	0.0	1.6
01/05/2005	1	0.0	1.4	0.0	0.0	1.4
31/07/2005	0	0.0	0.0	0.0	0.0	0.0
31/07/2005	0	0.0	0.0	0.0	0.0	0.0
31/07/2005	0	0.0	0.0	0.0	0.0	0.0
31/07/2005	0	0.0	0.0	0.0	0.0	0.0
31/07/2005	0	0.0	0.0	0.0	0.0	0.0
31/07/2005	0	0.0	0.0	0.0	0.0	0.0
31/07/2005	0	0.0	0.0	0.0	0.0	0.0
31/07/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	0	0.0	0.0	0.0	0.0	0.0
2-6/11/2005	1	0.0	0.4	0.0	0.0	0.4
08/02/2006	3	3.8	0.0	0.0	7.0	3.8
08/02/2006	3	5.0	1.2	0.0	9.1	6.2
08/02/2006	4	0.4	14.9	1.2	0.0	15.3
08/02/2006	4	4.6	19.1	12.3	18.9	23.7
08/02/2006	3	0.0	0.8	0.0	0.0	0.8
08/02/2006	2	2.8	0.0	0.0	0.0	2.8
08/02/2006	1	0.0	0.0	0.0	0.0	0.0
08/02/2006	2	0.0	4.6	0.0	0.0	4.6
20/06/2006	3	0.1	0.9	0.0	0.2	1.1
20/06/2006	3	4.2	0.2	0.0	1.2	5.6
20/06/2006	3	7.2	0.3	0.0	9.7	17.2
20/06/2006	1	0.0	0.0	0.0	0.2	0.2
20/06/2006	3	0.1	0.0	0.0	0.2	0.3
20/06/2006	0	0.0	0.0	0.0	0.0	0.0
20/06/2006	1	0.4	0.0	0.0	0.0	0.4
20/06/2006	1	1.8	0.0	0.0	0.0	1.8
20/06/2006	0	0.0	0.0	0.0	0.0	0.0

Anexo V

Bitácora de la estación de Limno

