Research Article

From coexistence to competitive exclusion: can overfishing change the outcome of competition in skates (Chondrichthyes, Rajidae)?

Natalia L. Ruocco[1,2], Luis O. Lucifora[1,3], Juan M. Díaz de Astarloa[1,4], Roberto C. Menni[1,5]
Ezequiel Mabragaña[1,5] & Diego A. Giberto[1,2]
[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina
[2]Instituto Nacional de Investigación y Desarrollo Pesquero, Paseo Victoria Ocampo
s/n B7602HSA, Mar del Plata, Argentina
[3]Instituto de Biología Subtropical, Universidad Nacional de Misiones, Centro de Investigaciones
del Bosque Atlántico (CeIBA), P.O. Box 9, Puerto Iguazú, Misiones, Argentina
[4]Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales
Departamento de Ciencias Marinas, Funes 3350, B7602AYL Mar del Plata, Argentina
[5]Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina

ABSTRACT. Competition for food could be a major force driving changes in the community structure of skates (Rajidae) subjected to fishing exploitation. Under this hypothesis, small skates are released from competition with larger skates after fishing has depleted the larger species. Here, we compare the abundance patterns of two sympatric skates with similar niches but different life histories, *Bathyraja albomaculata* (larger and slow-reproducing) and *Bathyraja macloviana* (smaller and faster-reproducing), before (1971, 1978) and after (1998-2004) a 108% increase in industrial bottom trawling on the southeastern South American shelf in order to test the prediction that *B. macloviana* should competitively exclude *B. albomaculata* after the increase in fishing mortality. In 1971 and 1978, there was no relationship between the abundance of both species, indicating that they coexisted over large scales. In 1998-2004, the relationship between the abundances of these skates was bell-shaped, indicating that both species increased in abundance at low densities until peaking, after which *B. albomaculata* decreased when *B. macloviana* became more abundant, consistent with resource competition. We tested whether food may be a potential limiting resource by comparing the diet of both species. The two species consumed mostly polychaetes, differing only in the consumption of polychaetes from the family Nephthyidae, which was much higher for *B. macloviana*. *Bathyraja macloviana* could replace *B. albomaculata* at high densities when food resources may become scarce. These results support the hypothesis that competition release is an important factor explaining the changes in skate communities in overexploited areas.

Keywords: *Bathyraja albomaculata*, *Bathyraja macloviana*, Rajidae, diet overlap, resource competition, elasmobranch fisheries, Argentina.

De la coexistencia a la exclusión competitiva: ¿Puede la sobrepesca cambiar el resultado de la competencia en rayas (Chondrichthyes, Rajidae)?

RESUMEN. La competencia por el alimento podría ser una fuerza importante detrás de los cambios en la estructura de las comunidades de rayas (Rajidae) bajo explotación pesquera. Según esta hipótesis, las rayas pequeñas son liberadas de la competencia por las rayas de mayor tamaño, al disminuir la abundancia de éstas últimas por la pesca. En este trabajo, se comparan los patrones de abundancia de dos rayas simpátricas con nichos similares pero con diferentes historias de vida, *Bathyraja albomaculata* (mayor y de reproducción lenta) y *Bathyraja macloviana* (más pequeña y de reproducción más rápida), antes (1971, 1978) y después (1998-2004) de un incremento del 108% en el arrastre de fondo industrial en la plataforma sudeste de América del Sur, para evaluar la predicción que *B. macloviana* excluiría competitivamente a *B. albomaculata* después del aumento en la mortalidad por pesca. En 1971 y 1978, no hubo relación entre las abundancias de ambas especies, indicando que, a escalas grandes, coexistían. En 1998-2004, la relación entre las abundancias de ambas especies tuvo forma de campana, indicando que ambas incrementaron su abundancia a densidades bajas

hasta alcanzar un máximo, a partir del cual la abundancia de *B. albomaculata* disminuyó a medida que aumentaba la de *B. macloviana*, patrón consistente con la competencia por uso de recursos. Se evaluó si el alimento puede ser un recurso limitante mediante la comparación de la dieta de ambas especies. Ambas especies consumieron predominantemente poliquetos y difirieron sólo en el consumo de poliquetos Nephthyidae, mucho mayor en *B. macloviana*. *B. macloviana* remplazaría a *B. albomaculata* a altas densidades, cuando el alimento podría ser escaso. Estos resultados apoyan la hipótesis de que la liberación de la competencia es un factor importante en los cambios en las comunidades de rayas sobreexplotadas.

Palabras clave: *Bathyraja albomaculata*, *B. macloviana*, Rajidae, solapamiento de dieta, competencia por recursos, pesquerías de elasmobranquios, Argentina.

Corresponding author: Luis O. Lucifora (luis.lucifora@gmail.com)

INTRODUCTION

Competitive interactions that structure communities are usually not accounted for in fisheries management. Fishing usually affects a number of species simultaneously, but fisheries are mostly managed focusing on the target population without taking into account species interactions or other community processes in which the target population plays a role (Pauly *et al.*, 2002; Pikitch *et al.*, 2004; Myers & Ottensmeyer, 2005). As a result, unforeseen fishing effects usually spread throughout marine communities with serious consequences (Jackson *et al.*, 2001; Jennings *et al.*, 2001; Worm *et al.*, 2006; Daskalov *et al.*, 2007; Myers *et al.*, 2007).

Skates (Rajidae), as a group, are highly affected by fisheries, but different species may differ in their response to fishery exploitation. Several species of skates have suffered large declines or even extirpation from large parts of their geographic range due to fisheries overexploitation (Brander, 1981; Casey & Myers, 1998; Graham *et al.*, 2001; Devine *et al.*, 2006). It is apparent that they vary in their capacity to withstand exploitation and the abundance of smaller species increases after fishing removes larger species. This has been hypothesized to be a result of competition release, which allows the smaller, faster-reproducing species to replace the largest ones. Walker & Heessen (1996), Walker & Hyslop (1998) and Dulvy *et al.* (2000) observed conspicuous shifts in the skate community of the North Sea, after decades of heavy fishing pressure. Dulvy *et al.* (2000) hypothesized that this shift was the result of competitive release, since small skate species replace the larger ones after fishing released small species from competition with large species, leading to shifts in community structure. Dulvy *et al.* (2000) suggested that food would be the limiting resource behind the competitive relationship of skates in the North Sea, since skates are all benthic feeders preying upon a variety of invertebrates and small fishes.

Competition is usually studied at small scales where experiments are feasible. Most of the best evidence for competition in vertebrate communities comes from small-scale experiments (in the scale of m^2 or at most hectares) and from small-bodied organisms, such as small fishes (Schmitt & Holbrook, 1999), lizards (Petren & Case, 1996) and small mammals (Meserve *et al.*, 1996). While controlled experiments provide the most unambiguous evidence for competition, their unfeasibility at large scales makes them impractical to study the importance of competition in large-scale communities (Connell, 1983).

As fisheries affect communities at a large scale (usually of hundreds or thousands of km^2), where controlled experimentation is not possible, other approaches must be taken to study how competition may structure marine communities and how fishing may interact with competition to affect ecological processes desired to be maintained. These alternative approaches have been successfully applied in large-scale studies to infer the presence of competition in both terrestrial (Creel & Creel, 1996; Cooper *et al.*, 2007) and marine (Ruggerone *et al.*, 2003) species.

In this paper we use an alternative, non-experimental, modelling approach to study competition at a large scale. Our approach compares the relationship between the abundance of two skates before and after the hyper-development of industrial trawl fishing on the southeastern South American shelf, in order to test Dulvy *et al.*'s (2000) hypothesis. The theoretical basis for our rationale is as follows. Over large-scale communities, without human exploitation, the patterns of species abundance are more constant than at smaller scales (Sommer & Worm, 2003). At this large scale, species coexist, even though they may suffer local extinctions or colonize new places at smaller scales within the large-scale community as a result of competition (Ritchie, 2003). In this community, the abundances of both species do not show any particular relationship. On the other hand, if fisheries affect the competitive relationship between skates, as suggested

by Dulvy *et al.* (2000), there should be a negative relationship between two competing skates, at least at high densities, when resources become scarcer (*i.e.* limiting).

The southeastern South American shelf, between 35º and 55ºS, contains a diverse skate fauna (Menni & Stehmann, 2000; Cousseau *et al.*, 2007) and is subjected to intense, unsustainable fishing exploitation by bottom trawlers since the early 1990s (Agnew *et al.*, 1999; Campagna *et al.*, 2006; Cañete, 2006). From 1990 to 1995 the fishing effort on this area increased by 108% (Campagna *et al.*, 2006), and present levels of fishing effort in the area, as estimated from fuel consumption, are among the highest in the world (Tyedmers *et al.*, 2005). This resulted in the overexploitation of many chondrichthyan and bony-fish populations (Carozza *et al.*, 2004; Cordo, 2004; Massa *et al.*, 2004; Wöhler *et al.*, 2004). Skates from this area are affected by at least four different bottom-trawl fisheries, both as a target and bycatch. The white-dotted skate, *Bathyraja albomaculata*, and the Patagonian skate, *B. macloviana*, are two common skates affected by these fisheries. Both species are targeted by the Islas Malvinas rajid fishery (Agnew *et al.*, 2000) and as bycatch in finfish trawlers targeting Argentine hake, *Merluccius hubbsi*, southern blue whiting, *Micromesistius australis*, hoki, *Macruronus magellanicus* (Brickle *et al.*, 2003), and red shrimp, *Pleoticus muelleri* (Cedrola *et al.*, 2005).

Bathyraja albomaculata attains 99 cm in total length and starts to reproduce at 10 years (Henderson *et al.*, 2004; Bücker, 2006). On the other hand, *B. macloviana* is the smallest species of the genus in the southwestern Atlantic, reaching 67 cm in total length and matures at 5-6 years (Bücker, 2006). Both species are specialized feeders, being polychaetes their dominant prey (Mabragaña *et al.*, 2005; Scenna *et al.*, 2006; Ruocco *et al.*, 2009), which results in a high dietary overlap suggestive of a potential competitive interaction between them (Brickle *et al.*, 2003). Thus, *B. albomaculata* and *B. macloviana* are a good model system to study the competitive release hypothesis in skates because both species suffer a similar fishing pressure, potentially overlap in the use of some resource (*i.e.* food) and have a large difference in age at maturity, with *B. macloviana* maturing at about half the age of *B. albomaculata*.

Here, we compare the abundance and diet of the white-dotted skate, *B. albomaculata*, and the Patagonian skate, *B. macloviana*, at a large scale -the southeastern South American shelf between 35 and 55ºS- before and after a major increase in fishing effort in order to test the hypothesis that competition may occur between the two species.

MATERIALS AND METHODS

Pre-fishing abundance patterns

Pre-fishing abundance patterns were estimated using data from 241 stations trawled during two research cruises carried out in 1971 and 1978 that covered the area from 37.9º to 54°S, at depths between 30 and 450 m (Fig. 1). Standard commercial 42.7 and 60.9 m wide bottom trawl nets were used in the 1971 and 1978 cruises, respectively, which were conducted by the same vessel. All tows lasted 30 min at a speed of 4 knots.

To explore the relationship between the abundance of *B. albomaculata* and *B. macloviana*, we constructed generalized linear models (GLM) with a log link and a negative binomial error distribution to account for the large number of zeros in the data and the dependance of the variance on the mean. All models included the number of individuals of *B. albomaculata* (N_{Ba}) as the dependent variable. N_{Ba} rather than the number of individuals of *B. macloviana* (N_{Bm}) was included as the dependent variable because Dulvy *et al.*'s (2000) hypothesis predicts that the larger and slower-reproducing species, in this case *B. albomaculata*, will be affected by the smaller and faster-reproducing species, in this case *B. macloviana*, after an increase in fishing pressure. All possible combinations of season (*S*; summer or winter), depth (*D*), latitude (*L*) and N_{Bm} were included as independent variables. To deal with nonlinear effects of *D* and N_{Bm}, models with quadratic terms (*i.e.* $D + D^2$ and $N_{Bm} + N_{Bm}^2$) were also fitted. We could not include log(swept area) as an offset variable (see below) for the pre-fishing analysis because we did not have that information for these cruises. However, as the data come from research cruises, all tows were performed in a standardized fashion, with swept area not expected to vary substantially between trawl stations.

Akaike's Information Criterion (AIC) were computed for each model. The most parsimonious model (*i.e.* hypothesis) was chosen as that with the lowest AIC (Franklin *et al.*, 2001; Johnson & Omland, 2004).

Post-fishing abundance patterns

A total of 452 trawling stations from 7 research cruises conducted between 1998 and 2004, from 35º to 55°S, at depths between 46 and 380 m were used in this analysis (Fig. 1). A 59 m Engel-type bottom-trawl net, with a stretched mesh size of 200 mm in the wings and 103 mm in the codend, a vertical height of 4 m, and a horizontal opening of 15 m was used in all research cruises. Each haul lasted 30 min and trawling speed was 3.6 knots. The surveys were aimed at the assessment of Argentine hake, *Merluccius hubbsi*, southern blue whiting, *Micromesistius australis*, hoki,
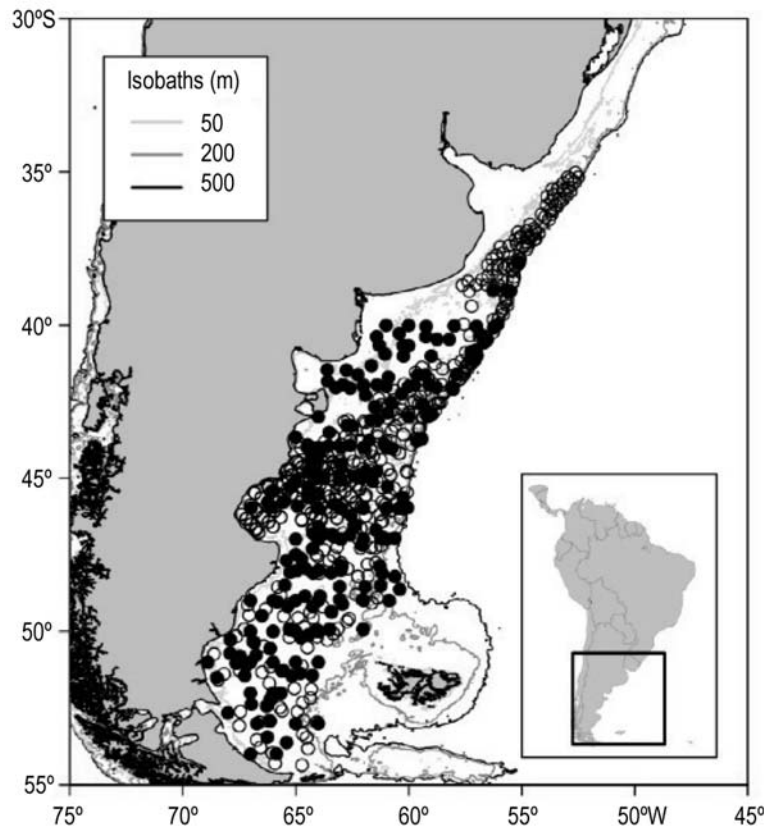
Figure 1. Southeastern South American shelf showing the location of pre-fishing (1971 and 1978, black circles) and post-fishing (1998-2004, white circles) trawl stations used in the analyses.

Figura 1. Plataforma continental de América del Sur con las estaciones de muestreo utilizadas en el análisis antes (1971 y 1978, círculos negros) y después (1998-2004, círculos blancos), del desarrollo de la pesquería.

Macruronus magellanicus, and Argentine squid, *Illex argentinus*.

As for the pre-fishing analyses, GLMs with a log link and a negative binomial distribution were used. All models included the number of *B. albomaculata* caught per trawl (N_{Ba}) as the dependent variable and the log of the swept area as an offset variable. All possible combinations of number of *B. macloviana* caught per trawl (N_{Bm}), latitude (l), depth (D), sin, cosine, $2 \times$ sin and $2 \times$ cosine of Julian day (d) were included as independent variables. Models with quadratic terms (*i.e.* $D + D^2$ and $N_{Bm} + N_{Bm}^2$) were also fitted. The best hypothesis was chosen using information theory in the same way as with the pre-fishing analyses, as the model with the lowest AIC.

Measurement error

In both pre- and post-fishing situations, the abundance of both *B. macloviana* and *B. albomaculata* were measured with error. This situation violates the assumption of GLMs that explanatory variables are measured without error. To deal with this situation, we reestimated the parameters for N_{Bm} in the cases when the best model included the terms N_{Bm} or $N_{Bm} + N_{Bm}^2$. We did this by using the simex method (Cook & Stefanski, 1994). Simex reestimates the parameters of the model through an iterative procedure that inflates the measurement error by a factor λ, creating several estimates (one for each value of λ) and extrapolating the estimation to the case of no measurement error. As the measurement error was unknown (no repeated sampling at the same time and place was performed), we repeated the simex procedure for a range of levels of measurement error extending over 4 orders of magnitude (*i.e.* standard error = 1, 10, 100 and 1000).

Dietary analysis

To evaluate if feeding habits were a possible overlapping resource between the two species, we analyzed the stomach contents of 89 specimens of *B. albomaculata* and 88 of *B. macloviana* caught in scientific surveys in the southwestern Atlantic between 37° and 55°S, over a depth range of 43-440 m, between 2000 and 2003. The net and trawl

specifications were the same as for the analysis of post-fishing abundance. For each specimen, total length and sex were recorded. The stomachs were removed, frozen and subsequently analyzed in the laboratory. Prey were identified to the lowest possible taxonomic level, counted and weighted to the nearest 0.01 g. Only 12 stomachs of *B. albomaculata* were empty. Sample sufficiency was assessed by constructing accumulation curves for the number of prey species as a function of the number of skates examined for stomach contents, after randomizing the sampling order 1000 times. Sample size was judged to be sufficient if the curves reached an asymptote.

The number of each prey group consumed by each individual was modeled as a function of species, sex, total length, latitude, depth and year in order to test for differences between species while controlling for the effects of the other variables. For each prey, a generalized linear model with a log link and a negative binomial error distribution was constructed (Lucifora *et al.*, 2009a, 2009b; Barbini & Lucifora, 2011). Afterwards, the best minimum model (BMM) was chosen by minimization of the AIC. Differences in diet between species were considered important if the variable species was included in the BMM. The magnitude of inter-specific differences in the consumption of a given prey was quantified by the BMM coefficient for the variable "species".

RESULTS

Pre-fishing abundance patterns

There was no relationship between the abundances of *B. albomaculata* and *B. macloviana* during 1971 and 1978, well before the development of intense industrial fishing (Fig. 2a). The best model explaining the abundance of *B. albomaculata* included the variables S, D and D^2, but not abundance of *B. macloviana*, indicating that both species coexisted at all densities of *B. macloviana*. The best model had the following parameters: intercept = -6.841, S(winter relative to summer) = 0.662, D = 0.054, D^2 = -0.0001 (AIC = 241.8).

Post-fishing abundance patterns

Between 1998 and 2004 there was a change in the interaction between *B. albomaculata* and *B. macloviana*, as compared to the pattern in 1971 and 1978. The abundance of *B. albomaculata* increased at low densities of *B. macloviana*, reached a peak and decreased at high densities of *B. macloviana* (Fig. 2b).

The best model describing the relationship of the abundances of *B. macloviana* and *B. albomaculata*
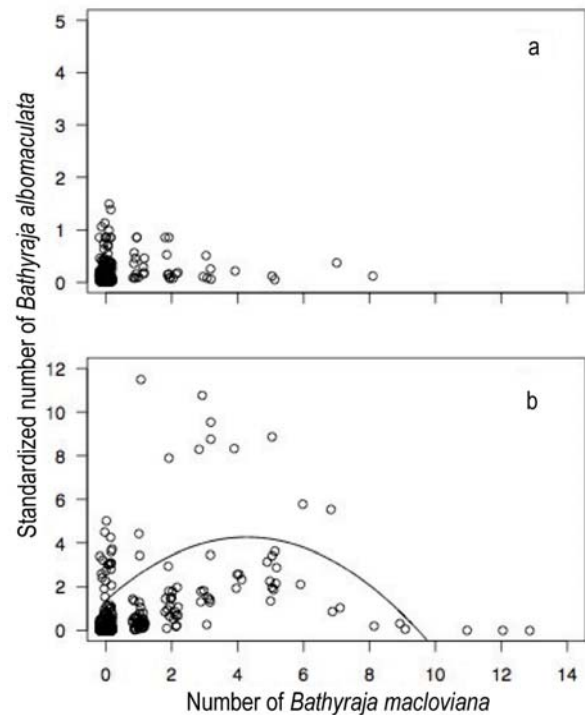

Figure 2. Relationship between the abundance of the skate *Bathyraja albomaculata* as a function of the abundance of *B. macloviana* on the southeastern South American shelf. a) Pre-fishing situation between 1971 and 1978, b) post-fishing situation between 1998 and 2004. White circles are fitted values for the best models in each situation. The solid line in (b) is the relationship estimated from a generalized linear model with a negative binomial error distribution and a log link. A small amount of jitter was added to the data in the plots (not in the analyses), to improve visualization of overlapping data points.

Figura 2. Abundancia de la raya *Bathyraja alboma-culata* en función de la abundancia de la raya *B. macloviana* en la plataforma del sudeste de América del Sur. a) Situación pre-pesca entre 1971 y 1978, b) situación post-pesca entre 1998 y 2004. Los círculos blancos son valores ajustados por los mejores modelos de cada situación. La línea continua en (b) es la relación estimada por el modelo lineal generalizado con distribución binomial negativa y enlace logarítmico. Para mejorar la visualización debido a la superposición de puntos, se movieron muy levemente algunos puntos (sólo para visualización, no para el análisis).

included L, $2 \times \sin(d)$, $\cos(d)$, D, D^2, N_{Bm} and N_{Bm}^2. The parameters of the model were: intercept = 0.321, L = -0.088, $2 \times \sin(d)$ = -0.846, $\cos(d)$ = -0.571, D = 0.067, D^2 = -0.0001, N_{Bm} = 1.346, N_{Bm}^2 = -0.157 (AIC = 552.55).

Application of the simex procedure did not lessen the effect of N_{Bm} and N_{Bm}^2, as their coefficients remained high. For each level of measurement error tried (1, 10, 100 and 1000), the coefficients for both parameters were 2.573 and -0.310, 1.588 and -0.226, 2.943 and -0.461, and 3.019 and -0.471, for N_{Bm} and N_{Bm}^2, respectively.

Dietary analysis

The most important prey found in both species were polychaetes, amphipods and isopods, while cirripeds, crabs, cumaceans, brittlestars and mollusks were the less consumed prey; for this reason these prey were grouped together for analysis as "other prey". Accumulation curves reached an asymptote for both species, indicating that sample size was sufficient to describe diet in each species (Fig. 3).

Diet was very similar in the two species; it only differed in the consumption of polychaetes of the family Nephthyidae which was 38 times higher in *B. macloviana*. The only two other prey with a different consumption among skate species were unidentified polychaetes (3 times as common in *B. macloviana* as in *B. albomaculata*) and other prey (0.4 times as common in *B. macloviana* as in *B. albomaculata*) (Fig. 4).

DISCUSSION

Our results are consistent with the hypothesis that competitive release allows fast-reproducing skate species to exclude slow-reproducing ones producing a shift in skate community structure after heavy fishing pressure (Dulvy *et al.*, 2000). In a non-equilibrium community, such as one subjected to a high fishing pressure, a medium-sized but smaller, faster-reproducing skate, *B. macloviana*, outcompetes a larger, slow-reproducing species, *B. albomaculata*, as proposed by Dulvy *et al.* (2000). This situation contrasts with the coexistence of both species at all densities observed during 1971 and 1978, well before the hyper-development of industrial fishing in the early 1990s that persists at present (Campagna *et al.*, 2006).

Coexistence is the rule in natural communities of mobile animals, even when competition occurs (Ritchie, 2003). Exclusive resources- *i.e.* those resources used solely by one of the competitors- allow species to coexist, even when both species compete for many other shared resources (Ritchie, 2003). Due to the lack of biological data during the pre-fishing years, we can only speculate about which resources were exclusively used by *B. macloviana* or *B. alboma-*
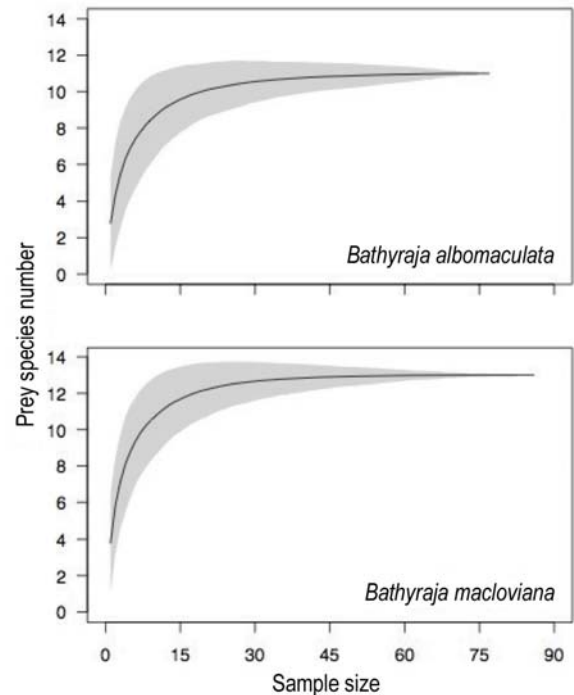

Figure 3. Accumulation curves for prey species of the skates *Bathyraja albomaculata* and *B. macloviana* on the southeastern South American shelf, as a function of number of skates examined for stomach contents. The solid line represents the mean number of prey species for a given sample size and the shaded area is ± 1 standard error, after 1000 permutations of the sampling order. The asymptote reached indicates that a sufficient number samples was examined.

Figura 3. Curvas acumulativas de especies presa de las rayas *Bathyraja albomaculata* y *B. macloviana* en la plataforma suroriental de América del Sur, en función del número de estómagos examinados. La línea continua representa el número medio de especies presa para un tamaño muestral determinado y el área sombreada corresponde a ± 1 error estándar, después de 1000 permutaciones del orden de muestreo. El alcance de una asíntota indica que se examinó un número suficiente de muestras.

culata that may have allowed coexistence of both species during the pre-fishing years. The almost exclusive use of Nephthyid polychaetes by *B. macloviana* suggests that they could have been used as an unshared resource, assuming that diet composition has not changed substantially from the pre-fishing to the post-fishing ecosystem state.

We propose that intense fishing pressure shifted the balance in favor of *B. macloviana* because of its earlier sexual maturation as compared to *B. albomaculata*. Given its earlier age at maturity –an important determinant of population growth and
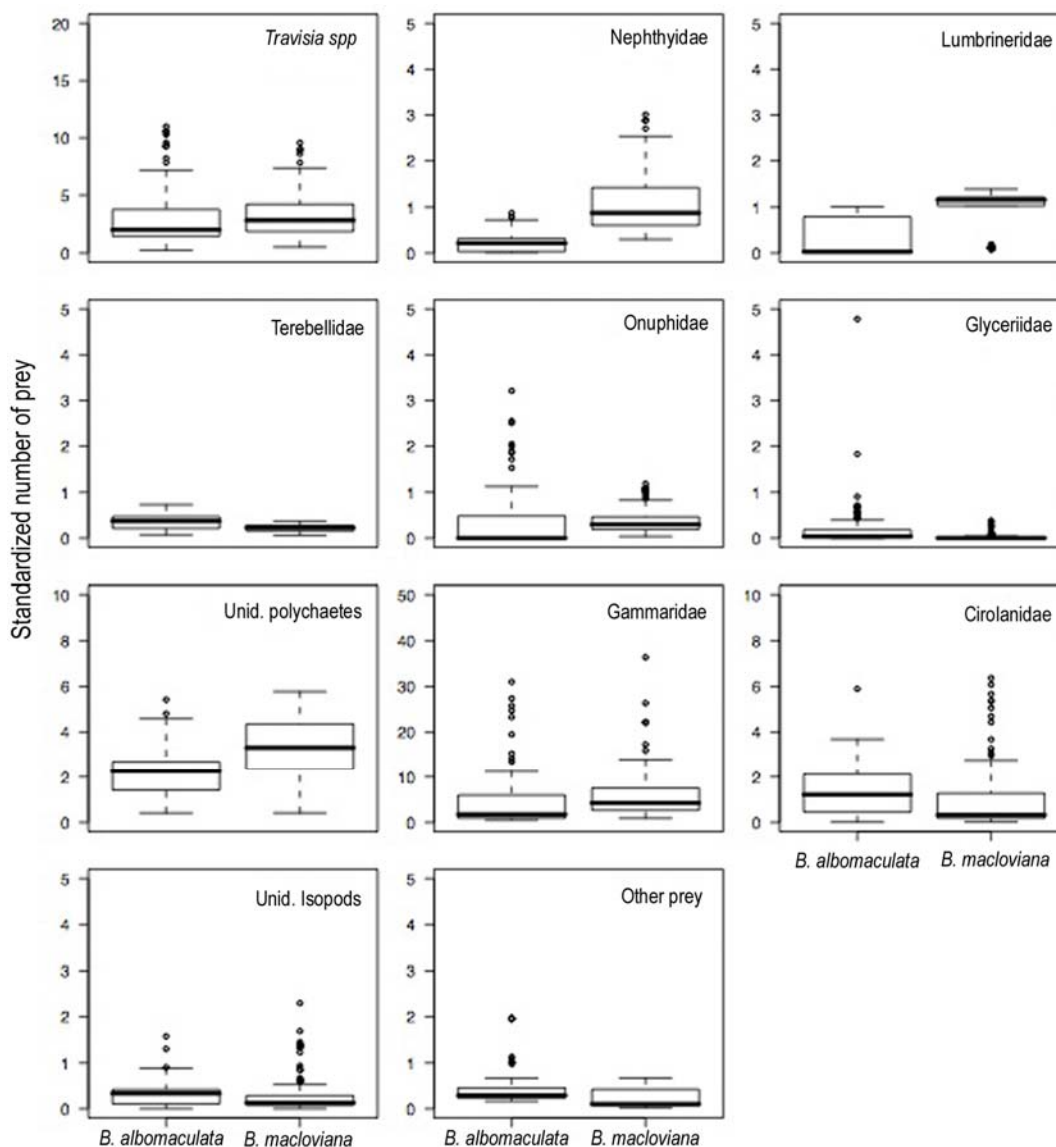
Figure 4. Comparative consumption of 11 prey groups by the skates *Bathyraja albomaculata* and *B. macloviana* on the southern South American shelf. Values are standardized by sex, total length, latitude, depth and year of sampling. Prey marked with an asterisk were consumed in significantly different amounts by the two species. Bold line: median; box: interquartile range; whiskers: range (1.5 times the interquartile range); circles: outliers.

Figura 4. Comparación del consumo de 11 grupos de presas de las rayas *Bathyraja albomaculata* y *B. macloviana* en la plataforma del suroriental de América del Sur. Los valores están estandarizados por sexo, longitud total, latitud, profundidad y año de muestreo. Las presas marcadas con un asterisco fueron consumidas en cantidades significativamente diferentes por las dos rayas. Línea gruesa: mediana; límites del recuadro: rango intercuartil; líneas: rango (1,5 veces el rango intercuartil); círculos: valores extremos.

recovery in many marine fishes (Myers *et al.*, 1997; Heppell *et al.*, 1999; Cortés, 2002; Reynolds *et al.*, 2005)– *B. macloviana* may cope better with fishing mortality than *B. albomaculata*. By having a higher productivity, *B. macloviana* may have a higher recolonization rate than *B. albomaculata* and replace it, once *B. albomaculata* was removed from a given area by fishing.

Resource competition, rather than interference competition, is consistent with the bell-shaped relationship between the abundance of *B. alboma-culata* and *B. macloviana* after the hyper-development of industrial fisheries on the southeastern South American shelf. At low densities, when resources are not limiting, the abundance of both species is positively correlated due to their similarity in resource

use, i.e. both species increase in sympatry because the shared resource is not limiting, since both species are at low densities. On the other hand, at high densities, when resources become scarcer, *B. macloviana* outcompetes *B. albomaculata*. The dominance of *B. macloviana* is due to their faster population dynamics which is explained by its earlier maturity (Bücker, 2006). Then, under a similar fishing pressure, the faster growing population dominates over the slower growing one. The dominance of *B. macloviana* (the smallest species) over *B. albomaculata* suggests that, as proposed by Dulvy *et al.* (2000), resource competition rather than interference competition is operating, since in interference competition usually the larger species dominates over the smaller one (Fedriani *et al.*, 2000; Valeix *et al.*, 2007).

Information on composition and distribution of benthic communities from the southeastern South American shelf is scarce and precluded any analysis of the potential effects of prey availability on the relationship between the abundances of *B. macloviana* and *B. albomaculata*. The only study that covered all our study area found three areas differing in their benthic assemblages (considering only mollusks, bryozoans and echinoderms): 36°-43°S and 43°-55°S below the 100 m isobath, and 39°-55°S beyond the 100 m (Bastida *et al.*, 1992). Information on polychaete distribution is available only for the southern (Bremec *et al.*, 2000; Montiel *et al.*, 2005 and references therein) and the northern (Bremec & Giberto, 2006) extremes of the study area. In those areas, polychaetes have an heterogeneous distribution, with some regions of low faunistic similarity due to differences in sediment composition and oceanographic conditions. The main prey of both *B. macloviana* and *B. albomaculata*, Opheliid polychaetes, are uncommon in some regions of the shelf, contributing with less than 5% of the total individuals sampled by Bremec *et al.* (2000) and Bremec & Giberto (2006). However, there is no comparable data of the density of these polychaetes that could be used to estimate the food availability for the skates. The potential effects of differences in spatial availability of prey on our results should be considered in future studies.

Other ecological processes, such as the negative effects of shared enemies (apparent competition; Bonsall & Hassell, 1997; Morris *et al.*, 2004), might contribute to explain the pattern between the abundance of both species observed as well. If *B. macloviana* is more resilient to some shared predator or parasite than *B. albomaculata*, when both species are in sympatry, these enemies will affect *B. alboma-*

culata more heavily than *B. macloviana*, resulting in the apparent exclusion of *B. albomaculata* by *B. macloviana*. This might occur, for instance, if both species differ in the ability to detect predators, as observed in stingrays (Semeniuk & Dill, 2006). Nothing is known on the effect of predators, parasites or other potential natural enemies on populations of species of *Bathyraja*, which precludes any evaluation of this hypothesis. However, although apparent competition might play some role in producing the observed pattern, the high similarity in diet of both species suggests that, at high densities, food can become a limiting resource, and then competition may operate.

We described an example of change in the relationship of abundances of two ecologically similar skate populations after intense exploitation. This example may indicate that intense industrial fishing pressure may produce shifts in competitive interactions that may lead to shifts in skate community structure. The pattern found for *B. albomaculata* and *B. macloviana* supports the hypothesis that skate communities may experience shifts in structure due to competitive release (Dulvy *et al.*, 2000), and give further reasons for an ecosystemic management of fisheries (Pauly *et al.*, 2002; Pikitch *et al.*, 2004; Myers & Ottensmeyer, 2005). Management of fisheries that affect skates should focus on the most sensitive species instead of the target species (Myers & Ottensmeyer, 2005) in order to avoid fishery-driven changes in skate communities and marine ecosystems.

The high speed of the changes in species interactions after overfishing –only 8-14 years after the commencement of large-scale industrial fishing in 1990– in a previously near-pristine region (Bortolus & Schwindt, 2007) calls for rapid action to avoid large-scale changes in ecosystem functioning.

ACKNOWLEDGEMENTS

REFERENCES

Agnew, D.J., C.P. Nolan, J.R. Beddington & R. Baranowski. 2000. Approaches to the assessment and management of multispecies skate and ray fisheries using the Falkland Islands fishery as an example. Can. J. Fish. Aquat. Sci., 57: 429-440.

Agnew, D.J., C.P. Nolan & J. Pompert. 1999. Management of the Falkland Islands skate and ray fishery. In: R. Shotton (ed.). Case studies of the management of elasmobranch fishes. FAO Fish. Tech. Paper, 378 part 1: 268-284.

Barbini, S.A. & L.O. Lucifora. 2011. Feeding habits of the Rio skate, *Rioraja agassizi* (Chondrichthyes: Rajidae), from off Uruguay and north Argentina. J. Mar. Biol. Assoc. UK, 91: 1175-1184.

Bastida, R., A. Roux & D.E. Martínez. 1992. Benthic communities of the Argentine continental shelf. Oceanol. Acta, 15: 687-698.

Bonsall, M.B. & M.P. Hassell. 1997. Apparent competition structures ecological assemblages. Nature, 388: 371-373.

Bortolus, A. & E. Schwindt. 2007. What would Darwin have written now? Biodiv. Conserv., 16: 337-345.

Brander, K. 1981. Disappearance of common skate *Raia batis* from Irish Sea. Nature, 290: 48-49.

Bremec, C.S., R. Elías & M.C. Gambi. 2000. Comparison of the polychaete fauna composition from the Patagonian shelf and the Strait of Magellan. Preliminary results from the cruises Shinkai Maru IV, V, X, and XI (1978-1979) and second Italian oceanographic cruise (1991). Bull. Mar. Sci., 67: 189-197.

Bremec, C.S. & D.A. Giberto. 2006. Polychaete assemblages in the Argentinean Biogeographical Province, between 34° and 38°S. Sci. Mar., 70: 249-257.

Brickle, P., V. Laptikhovsky, J. Pompert & A. Bishop. 2003. Ontogenetic changes in the feeding habits and dietary overlap between three abundant rajid species on the Falkland Inslands' shelf. J. Mar. Biol. Assoc. UK, 83: 1119-1125.

Bücker, A. 2006. Age and growth of skates of the genus *Bathyraja* in Argentina. M.Sc. Thesis, University of Bremen, Germany, 56 pp.

Campagna, C., C. Verona & V. Falabella. 2006. Situación ambiental en la ecorregión del Mar Argentino. In: A. Brown, U. Martínez-Ortiz, M. Acerbi & J. Corcuera (eds.). La situación ambiental argentina 2005. Fundación Vida Silvestre Argentina, Buenos Aires, pp. 323-337.

Cañete, G. 2006. La pesquería de merluza común. ¿Un ejemplo? In: A. Brown, U. Martínez-Ortiz, M. Acerbi & J. Corcuera (eds.). La situación ambiental argentina 2005. Fundación Vida Silvestre Argentina, Buenos Aires, pp. 337-342.

Carozza, C., C. Lasta, C. Ruarte, C. Cotrina, H. Mianzan & M. Acha. 2004. Corvina rubia (*Micropogonias furnieri*). In: R.P. Sánchez & S.I. Bezzi (eds.). El mar argentino y sus recursos pesqueros. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado de explotación. INIDEP, Mar del Plata, pp. 255-270.

Casey, J.M. & R.A. Myers. 1998. Near extinction of a large, widely distributed fish. Science, 281: 690-692.

Cedrola, P.V., A.M. González & A.D. Pettovello. 2005. Bycatch of skates (Elasmobranchii: Arhynchobatidae, Rajidae) in the Patagonian red shrimp fishery. Fish. Res., 71: 141-150.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat., 122: 661-696.

Cook, J.R. & L.A. Stefanski. 1994. Simulation-extrapolation estimation in parametric error measurement models. J. Am. Statist. Assoc., 89: 1314-1328.

Cooper, C.B., W.M. Hochachka & A.A. Dhondt. 2007. Contrasting natural experiments confirm competition between house finches and house sparrows. Ecology, 88: 864-870.

Cordo, H.D. 2004. Abadejo (*Genypterus blacodes*). Caracterización biológica y estado del recurso. In: R.P. Sánchez & S.I. Bezzi (eds.). El mar argentino y sus recursos pesqueros. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado de explotación. INIDEP, Mar del Plata, pp. 237-254.

Cortés, E. 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conserv. Biol., 16: 1048-1062.

Cousseau, M.B., D.E. Figueroa, J.M. Díaz de Astarloa, E. Mabragaña & L.O. Lucifora. 2007. Rayas, chuchos y otros batoideos del Atlántico sudoccidental (34°-55ºS). Publicaciones Especiales INIDEP, Mar del Plata, 102 pp.

Creel, S. & N.M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. Conserv. Biol., 10: 526-538.

Daskalov, G.M., A.N. Grishin, S. Rodionov & V. Minneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystems regime shifts. Proc. Nat. Acad. Sci., 104: 10518-10523.

Devine, J.A., K.D. Baker & R.L. Haedrich. 2006. Deep-sea fish qualify as endangered. Nature, 439: 29.

Dulvy, N.K., J.D. Metcalfe, J. Glanville, M.G. Pawson & J.D. Reynolds. 2000. Fishery stability, local extinctions, and shifts in community structure in skates. Conserv. Biol., 14: 283-293.

Fedriani, J.M., T.K. Fuller, R.M. Sauvajot & E.C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia, 125: 258-270.

Franklin, A.B., T.M. Shenk, D.R. Anderson & K.P. Burnham. 2001. Statistical model selection: an alternative to null hypothesis testing. In: T.M. Shenk & A.B. Franklin (eds.). Modeling in natural resource management: development, interpretation, and application. Island Press, Washington, pp. 75-90.

Graham, K.J., N.L. Andrew & K.E. Hodgson. 2001. Changes in relative abundance of sharks and rays on Australian south east fishery trawl grounds after twenty years of fishing. Mar. Freshw. Res., 52: 549-561.

Henderson, A.C., A.I. Arkhipkin & J.N. Chtcherbich. 2004. Distribution, growth and reproduction of the white-spotted skate *Bathyraja albomaculata* (Norman, 1937) around the Falkland Islands. J. Northw. Atl. Fish. Sci., 35: 79-87.

Heppell, S.S., L.B. Crowder & T.R. Menzel. 1999. Life table analysis of long-lived marine species with implications for conservation and management. In: J.A. Musick (ed.). Life in the slow lane. Am. Fish. Soc. Symp., 23: 137-148.

Jackson. J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi, C.H. Peterson, R.S. Steneck, M.J. Tegner & R.R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293: 629-638.

Jennings, S., T.A. Dinmore, D.E. Duplisea, K.J. Warr & J.E. Lancaster. 2001. Trawling disturbance can modify benthic production processes. J. Anim. Ecol., 70: 459-475.

Johnson, J.B. & K.S. Omland. 2004. Model selection in ecology and evolution. Trends Ecol. Evol., 19: 101-108.

Lucifora, L.O., V.B. García & A.H. Escalante. 2009a. How can the feeding habits of the sand tiger shark influence the success of conservation programs? Anim. Conserv., 12: 291-301.

Lucifora, L.O., V.B. García, R.C. Menni, A.H. Escalante & N.M. Hozbor. 2009b. Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. Ecol. Res., 24: 109-118.

Mabragaña, E., D.A. Giberto & C.S. Bremec. 2005. Feeding ecology of *Bathyraja macloviana* (Rajiformes: Arhynchobatidae): a polychaete-feeding skate from the south-west Atlantic. Sci. Mar., 69: 405-413.

Massa, A.M., L.O. Lucifora & N.M. Hozbor. 2004. Condrictios de las regiones costeras bonaerense y uruguaya. In: R.P. Sánchez & S.I. Bezzi (eds.). El mar argentino y sus recursos pesqueros. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado de explotación. INIDEP, Mar del Plata, pp. 85-100.

Menni, R.C. & M.F.W. Stehmann. 2000 Distribution, environment and biology of batoid fishes off Argentina, Uruguay and Brazil. A review. Rev. Mus. Arg. Cienc. Nat. n. ser., 2: 69-109.

Meserve, P.L., J.R. Gutiérrez, J.A. Yunger, L.C. Contreras & F.M. Jaksic. 1996. Role of biotic interactions in a small mammal assemblage in semiarid Chile. Ecology, 77: 133-148.

Montiel, A., D. Gerdes, B. Hilbig & W.E. Arntz. 2005. Polychaete assemblages on the Magellan and Weddell Sea shelves: comparative ecological evaluation. Mar. Ecol. Prog. Ser., 297: 189-202.

Morris, R.J., O.T. Lewis & H.C.J. Godfray. 2004. Experimental evidence for apparent competition in a tropical forest food web. Nature, 428: 310-313.

Myers, R.A., J.K. Baum, T.D. Shepherd, S.P. Powers & C.H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science, 315: 1846-1850.

Myers, R.A., G. Mertz & P.S. Fowlow. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. Fish. Bull., 95: 762-772.

Myers, R.A. & C.A. Ottensmeyer. 2005. Extinction risk in marine species. In: E.A. Norse & L.B. Crowder (eds.). Marine conservation biology: the science of maintaining the sea's biodiversity. Island Press, Washington, pp. 58-79.

Pauly, D.A., V. Christensen, S. Guénette, T.J. Pitcher, U.R. Sumaila, C.J. Walters, R. Watson & D. Zeller. 2002. Towards sustainability in world fisheries. Nature, 418: 689-695.

Petren, K. & T.J. Case. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. Ecology, 77: 118-132.

Pikitch, E.K., C. Santora, E.A. Babcock, A. Bakun, R. Bonfil, D.O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E.D. Houde, J. Link, P.A. Livingston, M. Mangel, M.K. McAllister, J. Pope &

K.J. Sainsbury. 2004. Ecosystem-based fishery management. Science, 305: 346-347.

Reynolds, J.D., N.K. Dulvy, N.B. Goodwin & J.A. Hutchings. 2005. Biology of extinction risk in marine fishes. Proc. Roy. Soc. B, 272: 2337-2344.

Ritchie, M. 2003. Competition and coexistence of mobile animals. In: U. Sommer & B. Worm (eds.). Competition and coexistence. Springer, Berlin, pp. 109-131.

Ruggerone, G.T., M. Zimmermann, K.W. Myers, J.L. Nielsen & D.E. Rogers. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. Fish. Oceanogr., 12: 209-219.

Ruocco, N.L., L.O. Lucifora, J.M. Díaz de Astarloa & C.S. Bremec. 2009. Diet of the white-dotted skate, *Bathyraja albomaculata*, in waters of Argentina. J. Appl. Ichthyol., 25 (Suppl. 1): 94-97.

Scenna, L.B., S.B. García de la Rosa & J.M. Díaz de Astarloa. 2006. Trophic ecology of the Patagonian skate, *Bathyraja macloviana*, on the Argentine continental shelf. ICES J. Mar. Sci., 63: 867-874.

Schmitt, R.J. & S.J. Holbrook. 1999. Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. Oecologia, 118: 76-86.

Semeniuk, C.A.D. & L.M. Dill. 2006. Anti-predator benefits of mixed-species groups of cowtail stingrays (*Pastinachus sephen*) and whiprays (*Himantura uarnak*) at rest. Ethology, 112: 33-43.

Sommer, U. & B. Worm. 2003. Synthesis: back to Santa Rosalia, or no wonder there are so many species. In: U. Sommer & B. Worm (eds.). Competition and coexistence. Springer, Berlin, pp. 207-218.

Tyedmers, P.H., R. Watson & D. Pauly. 2005. Fueling global fishing fleets. Ambio, 34: 635-638.

Valeix, M., S. Chamaillé-Jammes & H. Fritz. 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at water holes. Oecologia, 153: 739-748.

Venables, W.N. & B.D. Ripley. 2002. Modern applied statistics with S-Plus. Springer, New York, 495 pp.

Walker, P.A. & H.J.L. Heessen. 1996. Long-term changes in ray populations in the North Sea. ICES J. Mar. Sci., 53: 1085-1093.

Walker, P.A. & J.R.G. Hislop. 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. ICES J. Mar. Sci., 55: 392-402.

Wöhler, O.C., M.C. Cassia & J.E. Hansen. 2004. Caracterización biológica y evaluación del estado de explotación de la polaca (*Micromesistius australis*). In: R.P. Sánchez & S.I. Bezzi (eds.). El mar argentino y sus recursos pesqueros. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado de explotación. INIDEP, Mar del Plata, Argentina, pp. 283-306.

Worm, B., E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern, J.B.C. Jackson, H.K. Lotze, F. Micheli, S.R. Palumbi, E. Sala, K.A. Selkoe, J.J. Stachowicz & R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314: 787-790.