

# South American sea lion and spiny dogfish predation on artisanal catches of southern hake in fjords of Chilean Patagonia

Ana de la Torre, Renato A. Quiñones, Diego A. Miranda-Urbina, and Fidel Echevarría

de la Torre, A., Quiñones, R. A., Miranda-Urbina, D. A., and Echevarría, F. 2010. South American sea lion and spiny dogfish predation on artisanal catches of southern hake in fjords of Chilean Patagonia. – *ICES Journal of Marine Science*, 67: 294–303.

The South American sea lion (*Otaria flavescens*) is a pinniped known to interact with fisheries, potentially damaging gear and lowering catches. Predation by *O. flavescens* and spiny dogfish (*Squalus acanthias*) on artisanal southern hake (*Merluccius australis*) catches in fjords of Chilean Patagonia is estimated and compared. Observations were made in the Gulf of Ancud and Comau Fjord in southern Chile from October 2005 to September 2006. Losses of southern hake catches to *O. flavescens* predation were 1.6% of the total catch of the species, and to spiny dogfish predation were slightly higher, at 3.3%. The predation of both species on southern hake catches varied throughout the year, but was lower in summer. Both predators showed a preference for adult southern hake over juveniles. There was no significant relationship between predation on southern hake catches by the sea lion and the availability of adult and juvenile southern hake on longlines (AHCL). However, there was a significant relationship ( $p < 0.05$ ) between AHCL and spiny dogfish predation. Most *O. flavescens* interaction events (81.4%) were during longline retrieval. Our results showed minimal interactions between *O. flavescens* and the artisanal southern hake fishery in the area, so with the present abundance of *O. flavescens*, there is no justification for reducing the sea lion population by hunting.

**Keywords:** artisanal fisheries, Chilean fjords, *Merluccius australis*, *Otaria flavescens*, Patagonia, southern hake, *Squalus acanthias*.

Received 14 October 2008; accepted 18 August 2009; advance access publication 16 October 2009.

A. de la Torre and F. Echevarría: Departamento de Biología, Facultad de Ciencias del Mar, Universidad de Cádiz, Puerto Real 11510, Cádiz, Spain. R. A. Quiñones: Programa de Investigación Marina de Excelencia (PIMEX-Nueva Aldea), Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile, and Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Bilbao 449, Coyhaique, Chile. D. A. Miranda-Urbina: Instituto de Zoología, Universidad Austral de Chile, Casilla 567, Valdivia, Chile. F. Echevarría: Centro Andaluz de Ciencia y Tecnología Marina (CACYTMAR), Universidad de Cádiz, Puerto Real 11510, Cádiz, Spain. Correspondence to R. A. Quiñones: tel: +56 41 22 07 428; fax: +56 41 22 07 254; e-mail: rquinone@udec.cl

## Introduction

Conflicts between marine mammals and fisheries arise in various parts of the world where feeding sites overlap with fishing activity (Wickens, 1995). The impact of this interaction on pinniped populations and fisheries varies widely (Wickens, 1995; Baraff and Loughlin, 2000; Kauppinen *et al.*, 2005), and it appears to be increasing as a consequence of the intensification of coastal fisheries worldwide (Harwood, 1987) and the global decline of fish populations, mainly through overfishing (Worm *et al.*, 2006). Typical negative direct interactions include (Lowry, 1982; Wickens, 1995): (i) pinniped mortality through bycatch; (ii) deliberate harming of pinnipeds by fishers (shooting at or hitting them); (iii) lost or damaged catches; (iv) lost or damaged fishing gear; and (v) alterations to the fishing operation. On the other hand, indirect biological interactions include competition for the same resource, changes in prey size structure and distribution, or changes in community composition resulting from fishing (Lowry, 1982; Beverton, 1985; Harwood, 1987; Shima *et al.*, 2000; Fertl, 2002).

In Chile, the South American sea lion (*Otaria flavescens*) is the only pinniped known to cause damage during fishing operations (Oliva *et al.*, 2003). As with other pinnipeds, the South American sea lion has learned to follow fishing vessels (Szteren

and Páez, 2002; Hückstädt and Antezana, 2003) and to take advantage (i.e. energy saving; Northridge, 1985) of the concentration of food available on fishing gear. When pinnipeds feed on the catches, the fishing gear may be damaged and the catch itself impacted (Torres *et al.*, 1979).

Chile has the most South American sea lions of any country, with an estimated abundance of about 150 000; the population has been growing over the past 10 years (Sielfeld *et al.*, 1997; Aguayo-Lobo *et al.*, 1998; Oporto *et al.*, 1999; Venegas *et al.*, 2001; Sepúlveda *et al.*, 2007; Bartheld *et al.*, 2008, Oliva *et al.*, 2008). Although there is no complete census of the sea lion population in Chilean Patagonia, the subpopulation there seems to be increasing, at least in the northern part of Patagonia, where there has been a growth of about 3000 sea lions over the past 10 years (Oliva *et al.*, 2008).

Fishers from Chilean Patagonia have reported interactions between the artisanal southern hake (*Merluccius australis*) fishery and the South American sea lion. The perception of the artisanal fishers is that such interactions are a key factor in explaining their decreased catches and income, so they have requested that fishing authorities establish measures for reducing the sea lion population by allowing hunting (Sepúlveda *et al.*, 2007). However, no quantitative information is available to assess this interaction effectively.

In addition, there is an interaction between the southern hake fishery and the spiny dogfish (*Squalus acanthias*), which preys on longline catches. Spiny dogfish make up part of the bycatch of several South American longline fisheries (Lamilla *et al.*, 2005; Seco Pon and Gandini, 2007). No information is available on the abundance of *S. acanthias* in Chile, but the South American subpopulation has decreased by about 30%, and the species is classified as vulnerable (Fordham *et al.*, 2006). In Chile, most commercial catches of *S. acanthias* are made in southern fjords by the artisanal fleet. The biggest annual landing of the species was in 1980, a total of 1189 t, after which annual landings decreased, fluctuating between 3 and 400 t (Gómez *et al.*, 2007). In the Patagonian fjords, the official catches of spiny dogfish are <100 t per year at the moment, but there are no estimates of mortality through bycatch or discarding (Lamilla *et al.*, 2005). Although spiny dogfish are known to be associated with the southern hake fishery, there is currently no record of the extent of its predation on southern hake caught by the longlines of the artisanal fleet.

In this context, the goals of this research are (i) to estimate predation on the artisanal catches of southern hake by South American sea lions and spiny dogfish, and (ii) to describe the behaviour of the South American sea lion during artisanal fishing operations targeting southern hake.

## Material and methods

The study was carried out on board artisanal fishing vessels operating in the Gulf of Ancud and the Comau Fjord (42°10'S 72°40'W; Figure 1). There are three non-breeding colonies (i.e. lacking pups year-round; Sielfeld *et al.*, 1997) in the study area: Liliguapi Island, Cahuelmó Fjord, and Pelada Island (Figure 1). On average, ~1500 sea lions were estimated to be distributed between the three rookeries during the period of this study, with a variable number throughout the year. Liliguapi Island in particular is subject to great variability in numbers, ranging from 6 to 2114 in different seasons. Cahuelmó Fjord and Pelada Island

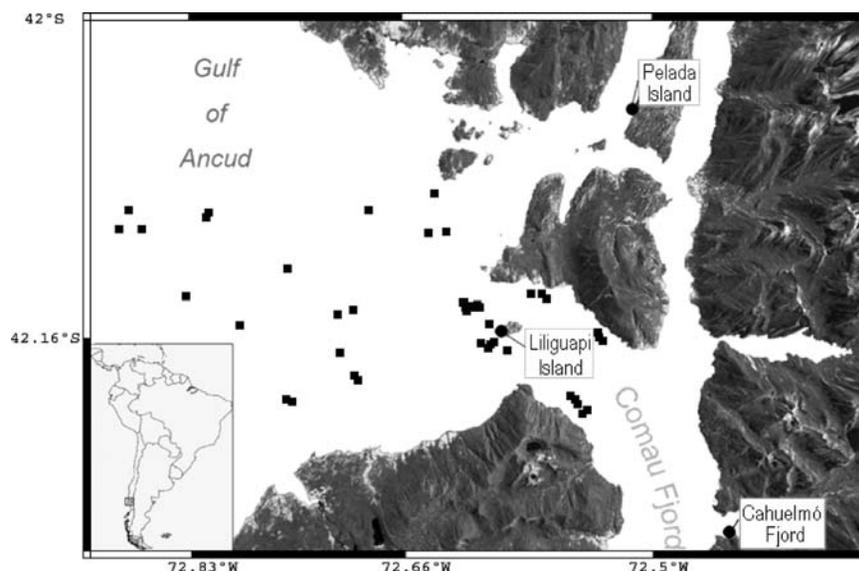
generally hold more stable populations, ranging from 55 to 480 and from 3 to 94 sea lions, respectively (AdIT, pers. obs.).

## Sampling and data collection

In all, 48 fishing events were observed between October 2005 and September 2006 (Figure 1): 12 in spring, 28 in summer, 6 in autumn, and 2 in winter. The dates of the fishing events depended on the monthly opening dates for the southern hake fishery, which are established by the Chilean fishing authority. One observer worked per vessel and, on average, two observers conducted simultaneous observations on board different vessels during a given month. In summer, longlines are set in the morning and retrieved in the evening. In winter, this is usually done over two consecutive days, setting the line on one day and retrieving it the next. Operationally, we define a fishing event as the period between the setting of a longline and its retrieval.

The longline consists of a horizontal main line with a variable number of hanging vertical lines (10–60 snoods). Each snood has a variable number of baited hooks (14–65). The longline is set between 150 and 350 m deep using two different designs: a hand-held guideline system (the main line set to remain at the surface), and a longline retained system (the main line set to remain at 150–350 m). The bait used was largely fresh, frozen, or salted sardine (*Strangomera bentincki* or *Sprattus fueguensis*), juvenile hake, and Patagonian grenadier (*Macruronus magellanicus*) obtained from the catches, but even salmon (*Salmo salar*) in some cases.

Observations were made by eye on board the vessels. The following information was recorded: (i) the date of the fishing event, (ii) the length of time the fishing gear remained in the water (i.e. the time elapsed between setting and retrieval;  $T_{i-w}$ ), (iii) the total number of hooks set on the longlines per fishing event ( $N_{hook}$ ), (iv) the total catch of adult and juvenile southern hake, undamaged, by number ( $N_h$  caught) and biomass, (v) the bycatch of other species by number, (vi) the number of adult and juvenile southern hakes preyed on or damaged by sea lions, and (vii) the number of adult and juvenile southern hake preyed



**Figure 1.** Map of the study area, showing the location of the 48 sampled artisanal fishing operations (black squares), and the three non-breeding sea lion colonies (black circles).

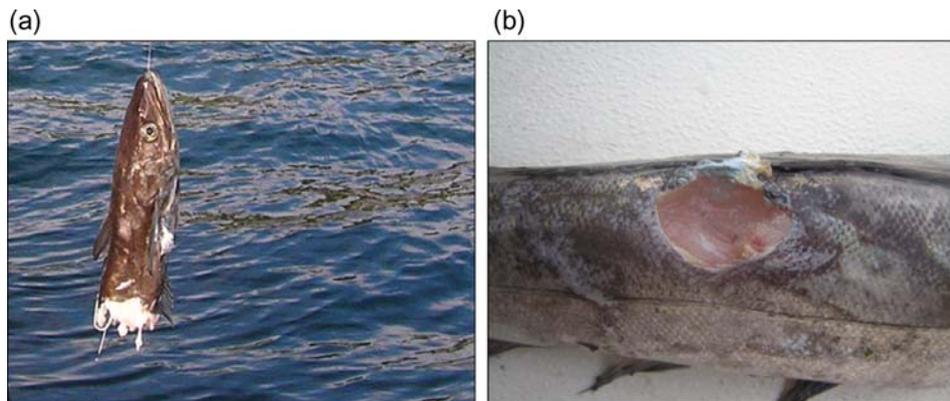
on or damaged by spiny dogfish. For each period of observation, we recorded the number of sea lions present around the vessel at all times, the time of the observation, how long each sea lion remained around the vessel, the animal's age class and sex (adult male, juvenile female, undetermined), and its behaviour (surface feeding, swimming, passing by, tugging on the snoods). The age class and the sex were determined based on descriptions of morphological characteristics in the literature (Sielfeld, 1983; Aguayo-Lobo *et al.*, 1998). We counted juveniles and females together because the animals spent very little time out of the water, and the morphological characteristics necessary for age and sex classification were not always visible. The vessel name, registration number, and length, and the geographic coordinates of the observation site were also recorded.

We operationally defined juvenile southern hake as those  $\leq 60$  cm total length. Losses of southern hake catches caused by sea lions and spiny dogfish were quantified by identifying the number of hake preyed upon or damaged by each predator, distinguishing between their different bite marks, which were identified on board once the catch had been retrieved and recovered. Before data collection, the characteristic bite marks made by sea lions and spiny dogfish on hake were verified *in situ* during seven fishing events. Sea lion bites tear the fish, are not precise, and do not avoid the spine. Spiny dogfish bites, on the other hand, are many, smaller, and avoid the dorsal spine (Figure 2). On several occasions, hake were caught with spiny dogfish attached to them. Although fishers from other parts of southern Chile (e.g. Chiloe Island) have reported a third type of bite ("knifed") that is inflicted by jumbo squid (*Dosidicus gigas*), we did not record any catch losses attributable to this predator in our study.

The dynamics of the southern hake fishery are mainly regulated by fishing restrictions (monthly catch quotas), weather, and yields. During the study, fishing events for the whole fleet were usually limited by weather to no more than 4–7 d per month; no fishing events took place in April and June. In August, the southern hake fishing season was closed as a result of a biological ban.

The southern hake (*M. australis*) catch was generally recorded as the number of fish and the biomass (kg; weighed on land). Fishing effort ( $E$ ) was calculated from

$$E = T_{i-w} \times N_{\text{hook}} \quad (1)$$



**Figure 2.** Characteristic damage to hake by (a) South American sea lions, and (b) spiny dogfish when the hake is hanging from longlines.

The cpue was calculated for adult southern hake ( $cpue_{\text{adult}}$ ), juvenile southern hake ( $cpue_{\text{juv}}$ ), and for combined adult and juvenile southern hake ( $cpue_{\text{total}}$ ; Table 1).

## Fishery–predator interactions

### Loss of the hake catch to South American sea lions and spiny dogfish

We recorded the losses of southern hake catches to sea lions and spiny dogfish as the number of adult and juvenile hake preyed upon or damaged by these animals. To compare predation by sea lions and spiny dogfish, we operationally defined a Sea Lion Standardized Predation Index (SLSPI) and a Spiny Dogfish Standardized Predation Index (SDSPI; Table 1). Variations in predation were studied considering the total, adult, and juvenile indices separately ( $SLSPI_{\text{total}}$ ,  $SLSPI_{\text{juv}}$ ,  $SLSPI_{\text{adult}}$ ,  $SDSPI_{\text{total}}$ ,  $SDSPI_{\text{juv}}$ , and  $SDSPI_{\text{adult}}$ ).

We also analysed variations in sea lion and spiny dogfish predation on hake catches relative to the availability of adult and juvenile hake on the longline (abbreviated here to AHCL; Table 1) and the fishing effort ( $T_{i-w}$  and  $N_{\text{hook}}$ ) using linear regression (Table 2). As fishing events with no predation could be related to the absence of the predator from the study area, information collected during such events was omitted from the analysis.

We analysed the trophic selectivity on two age classes (i.e. adult and juvenile) of southern hake by sea lions and spiny dogfish using the Chesson Selectivity Index ( $\alpha$ ; Chesson, 1978, 1983):

$$\alpha_i = \frac{(r_i/p_i)}{\sum_{i=1}^n (r_i/p_i)}, \quad i = 1, \dots, n, \quad (2)$$

where  $\alpha_i$  is the selectivity for prey  $i$ ,  $r_i$  the relative abundance of prey category  $i$  in the predator's diet,  $p_i$  the relative abundance of prey category  $i$  available in the environment, and  $n$  is the number of prey categories available ( $n = 2$ , adult and juvenile).

For our purposes, the proportion of prey category  $i$  in the predator's diet was taken to be the proportion of that age category preyed upon or damaged by the predator and recovered during the fishing operation, and the proportion of prey category  $i$  available in the environment was taken to be the proportion caught on the longlines. For this, we used the indices  $SLSPI_{\text{juv}}$ ,  $SLSPI_{\text{adult}}$ ,  $SDSPI_{\text{juv}}$ , and  $SDSPI_{\text{adult}}$  (Table 1), considering predation on adult and juvenile hake separately. An  $\alpha_i = 1/n$  (i.e. 0.5) indicates no selectivity

(the prey is consumed according to its availability in the environment),  $\alpha_i > 1/n$  indicates preference for the prey, and  $\alpha_i < 1/n$  indicates that the predator avoids the prey (Chesson, 1978, 1983).

Specific data on the age category (adult or juvenile) of the hake preyed upon by sea lions or spiny dogfish were lacking for some fishing events, so those events were not incorporated into the trophic selectivity analysis ( $n = 34$  fishing events). South American sea lion and spiny dogfish predation on the AHCL were compared between the two longline setting systems used, viz. hand-held guides or retained. This information was not recorded for three of the fishing events, so this comparison included just 45 of the 48 fishing events.

**Behaviour of sea lions during fishing events**

The observation effort was taken to be the minutes of observation during each fishing event while actually at the fishing site. The recorded observations were classified as sightings without

**Table 1.** Summary of equations for calculating the cpue and predation on southern hake catches by *O. flavescens* and *S. acanthias*.

Catches of southern hake	
$cpue_{adult} = N h_{adult} caught / (T_{i-w} \times N_{hook})$	
$cpue_{juv} = N h_{juv} caught / (T_{i-w} \times N_{hook})$	
$cpue_{total} = (N h_{total} caught) / (T_{i-w} \times N_{hook})$	
Availability of adult and juvenile hake on the longline (AHCL)	
$AHCL_{adult} = N h_{adult} catches + N h_{adult} preyed on by sea lions + N h_{adult} preyed on by spiny dogfish$	
$AHCL_{juv} = N h_{juv} catches + N h_{juv} preyed on by sea lions + N h_{juv} preyed on by spiny dogfish$	
$AHCL_{total} = N h_{total} catches + N h_{total} preyed on by sea lions + N h_{total} preyed on by spiny dogfish$	
Predation on southern hake catches by South American sea lions (SL)	
$SLSPI_{adult} = N h_{adult} preyed on by sea lion / AHCL_{adult}$	
$SLSPI_{juv} = N h_{juv} preyed on by sea lion / AHCL_{juv}$	
$SLSPI_{total} = N h_{total} preyed on by sea lion / AHCL_{total}$	
Predation on southern hake catches by spiny dogfish (SD)	
$SDSPI_{adult} = N h_{adult} preyed on by spiny dogfish / AHCL_{adult}$	
$SDSPI_{juv} = N h_{juv} preyed on by spiny dogfish / AHCL_{juv}$	
$SDSPI_{total} = N h_{total} preyed on by spiny dogfish / AHCL_{total}$	

$N h_{adult}$  is the number of adult hake,  $N h_{juv}$  the number of juvenile hake, and  $N h_{total}$  the total number of adult and juvenile hake ( $N h_{adult} + N h_{juv}$ ). To determine the variation in cpue throughout the year, the average cpue was calculated by month. October was excluded from the analysis because only one fishing event was observed then, and it resulted in extremely high catch rates (430 kg adult hake, 35 kg juvenile hake). Variations in predation by sea lions and spiny dogfish on the southern hake available on the longlines (AHCL) were studied by calculating the average SLSPI and SDSPI indices by month, taking total, adult, and juvenile indices separately.

interaction when the individual sea lion or group was swimming in or passing by the area of the fishing operation, and as interaction events when the pinnipeds fed at the surface or clearly tugged the longline. The main types of sea lion behaviour around the fishing operation were analysed by comparing the relative frequencies of each type of observation (sightings without interaction, interaction events).

The time the sea lion remained around the fishing operation was classified as: (i) <1 min, (ii) 1–9 min, (iii) 10–19 min, (iv) 20–60 min, and (v) >60 min. The relative frequencies of sightings were compared in the different ranges, taking into consideration fisher reactions.

To determine whether the sea lions had any preference for the viscera, bites were recorded as those affecting the viscera and those affecting any other body part.

To identify the phase of the fishing operation associated with the maximum interaction between sea lions and fishing, we compared both the number of sightings and the interaction events during the following phases of the fishing activity: (i) longline setting, i.e. the period when the fisher baits the hooks and releases the longlines into the water; (ii) longline in water, i.e. the period between setting and retrieval, when fishers are inactive; (iii) longline retrieval, i.e. the period when the catch is recovered; (iv) simultaneous longline setting and retrieval operations on one fishing boat (SSR), periods when one fisher was retrieving and another setting on the same vessel at the same time.

**Assessing the effect of the distance between fishing events and the sea lion rookery**

We analysed the degree of interaction between fishing events and distance from the rookery for Lilliguapi Island. That site was selected because: (i) it is a permanent rookery, (ii) it is closest to the preferred fishing area (Figure 1), and (iii) it has the largest number of sea lions throughout the year. Fishing events and the resting rookery were identified on navigation charts 7340 and 7300 of the Hydrographic and Oceanographic Service of the Chilean Navy (SHOA). The distances were measured using ArcGIS 9 software from ESRI (Environmental Systems Research Institute, Inc.). The distance between the fishing event and the rookery was categorized as 0–5000, 5000–10 000, or >10 000 m.

**Statistical analysis**

Comparisons between averages of two groups were conducted with a Student’s *t*-test. Comparisons of more than two groups were made with a one-way analysis of variance (Zar, 1999). Simple and multiple linear regressions were also conducted. Forward stepwise regressions were made according to Netter

**Table 2.** Regression models related to the predation by South American sea lions and spiny dogfish on southern hake artisanal catches.

Dependent variable	Independent variable	Model	$r^2$	$p$ -value
Simple linear regression				
$N h_{total} preyed on by sea lions$	AHCL <sub>total</sub>	–	0.00	0.82
$N h_{total} preyed on by sea lions$	$T_{i-w}$	–	0.04	0.33
$N h_{total} preyed on by sea lions$	$N_{hook}$	–	0.04	0.33
$\ln(N h_{total} preyed on by spiny dogfish + 1)$	AHCL <sub>total</sub>	$y = 0.008x + 0.271$	0.53	<b>0.000</b>
Forward stepwise regression				
$N h_{total} caught$	$T_{i-w} \cdot N_{hook}$	$y = -24.857 + 0.027 T_{i-w} + 0.158 N_{hook}$	0.64	<b>0.000</b>
$\ln(N h_{total} preyed on by spiny dogfish + 1)$	$T_{i-w} \cdot N_{hook}$	$y = -0.876 + 0.001 T_{i-w} + 0.001 N_{hook}$	0.59	<b>0.000</b>

Emboldened values denote  $p < 0.001$ . Logarithmic transformation was necessary for the spiny dogfish data to comply with the assumption of normality.

et al. (1996). A Kruskal–Wallis test was used to assess the effect of the distance between fishing events and the nearest sea lion rookery.

## Results

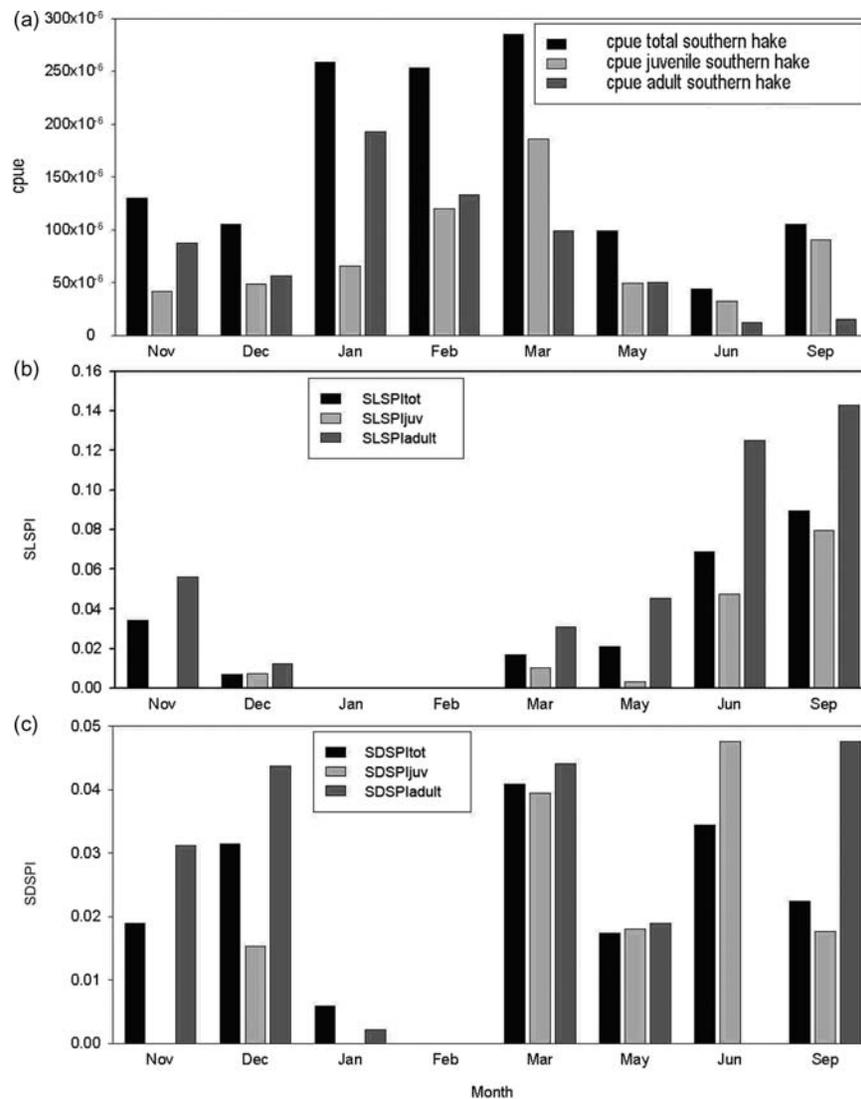
### Southern hake catches

The artisanal fishery caught 9757 kg (adults 7878 kg; juveniles 1879 kg) of southern hake during the 48 fishing events studied, an amount representing 74% of the total catch during these fishing events. Total southern hake catch rates ( $cpue_{total}$ ) as well as the catch rates of adults and juveniles varied throughout the year, increasing in summer (January–March) compared with the rest of the year (Figure 3a).

Forward stepwise regressions between southern hake catches and (i) the time the longline was submerged in the water from setting to retrieval, and (ii) the number of hooks set, were statistically significant (Table 2). The two variables ( $T_{i-w}$  and  $N_{hook}$ ) contributed significantly to the model.

### Losses of southern hake to predation by sea lions

South American sea lions were observed preying on adult and juvenile hake catches in 25 of the 48 fishing events (52.1%), with an average of 2.3 southern hake (s.d. 4.3) and a maximum of 25 preyed on per event. The proportion (in number of fish) of southern hake preyed on by sea lions during the study period represented 1.6% of the total catch of southern hake made during the same fishing events. Sea lion predation on the AHCL varied throughout the year, and was highest in winter. In summer (January and February), no important losses of AHCL attributable to sea lion predation were observed (Figure 3b). There was no significant relationship, however, between AHCL and predation by sea lions (Table 2). We evaluated the possibility that behavioural changes (e.g. feeding patterns, spatial displacement) during the sea lion's reproductive period could have influenced the outcome of the study by excluding summer (January–March) fishing events from the analysis. Nonetheless, the results were similar to those obtained for the entire year ( $r^2 = 0.00\%$ ,  $p = 0.99$ ).



**Figure 3.** (a) Cpue of southern hake, (b) SLSPI on hake, and (c) SDSPI on hake, recorded during the fishing events studied (total, adults, juveniles). For (b) and (c), the SPI total is not equal to the sum of adults plus juvenile hake; as it was not always possible to differentiate between them, they were pooled in the total category, increasing the denominator term availability (AHCL).

The South American sea lion was selective by age class, preferring adult southern hake throughout the entire study period, according to the Chesson Selectivity Index ( $\alpha$ ; Table 3). However, when sea lion predation was at its least, only one southern hake (an adult) was preyed upon, and in winter, only two fishing events took place, so winter values of  $\alpha$  might not be fully representative.

The correlation between sea lion predation on AHCL and fishing effort was not significant (Table 2). Predation by sea lions on the AHCL when using hand-held guides was slightly less than when using retained fishing gear, but this difference was not significant ( $t = -0.75$ ,  $p = 0.46$ ).

### Behaviour of sea lions during fishing events

In all, 164 observations on sea lion behaviour were made during 27 of the 48 studied fishing events. Slightly fewer interaction events (42.7%; tugging 34.2% and surface feeding 8.5%) were recorded than sightings without interaction (57.3%; passing by 12.8% and swimming 44.5%). These numbers suggest that, during many fishing events, sea lions approached the fishing operation and, despite the availability of southern hake on the longline, did not damage the catches, but rather swam around the area of operation. The percentage of fishing events with an interaction rose to 58.3% when those fishing events in which we recorded southern hake predation or damage by sea lions were included, although no sea lions were observed near the fishing operation. Most of the sea lion sightings (61.6%) were during gear retrieval; this was also the phase with the most interaction events (81.4%).

**Table 3.** Chesson Index ( $\alpha$ ) for selectivity of South American sea lions and spiny dogfish on adult and juvenile southern hake for different periods during the study.

Period and parameter	South American sea lion		Spiny dogfish	
	$\alpha_{\text{adult}}$	$\alpha_{\text{juv}}$	$\alpha_{\text{adult}}$	$\alpha_{\text{juv}}$
Whole study period (November 2005 – September 2006); South American sea lions, 34 fishing events; spiny dogfish, 33 fishing events <sup>a</sup>	0.58	0.42	0.61	0.39
Period of minimal sea lion and dogfish predation on the catch (January and February) <sup>b</sup>	1	0	1	0
Period excluding the months of minimal sea lion and spiny dogfish predation on the catch (November, December, March – September)	0.70	0.30	0.53	0.47
Breeding period of both predators (December – March)	0.58	0.42	–	–
Non-breeding period of both predators (November, April – September)	0.64	0.36	–	–
Period with the greatest proportion of juveniles in the catch composition (June – September)	0.65	0.35	0.61	0.39

<sup>a</sup>Fishing event 42 (March) was omitted from the analysis because of the abnormally large number of adult and juvenile hake preyed on by this predator; this outlier could have altered the results ( $N_{\text{hadult}}$  preyed on by spiny dogfish = 22;  $N_{\text{hjuv}}$  preyed on by spiny dogfish = 44).

<sup>b</sup>During the period of least spiny dogfish predation on the catch, only one southern hake (an adult) was preyed upon or damaged by this shark and, in winter, observations were only recorded during two fishing events, so the  $\alpha$  values may not be representative.

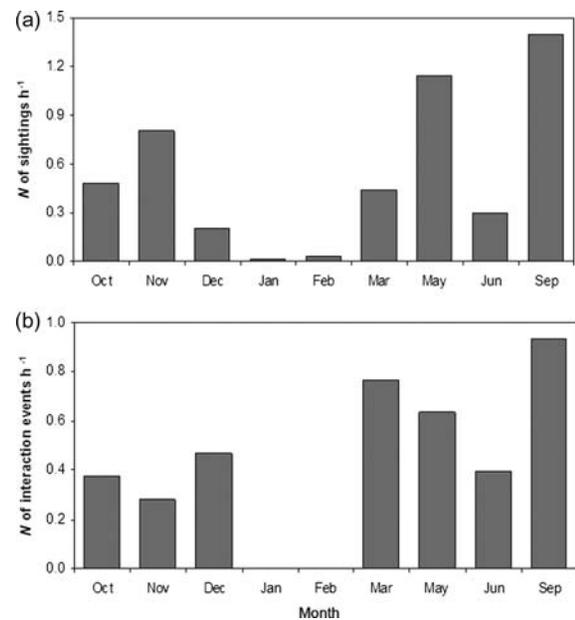
The number of sea lion sightings around fishing operations throughout the year decreased significantly in summer (Figure 4a), and no interaction events were recorded then (Figure 4b). When excluding summer from the analysis, the average number of sightings without interaction was  $0.58 \text{ h}^{-1}$ , exceeding the average number of sightings with an interaction ( $0.15 \text{ h}^{-1}$ ). In 75% of the cases observed, sea lions remained around the fishing operation for  $<10 \text{ min}$ ; they remained for longer than 1 h on just four occasions. The longer the sea lion remained around the fishing operation, the more likely it was that the fishers would try to chase them away by throwing bait into the water, suspending the fishing operation, shooting at them, and/or trying to scare them with noises. In general, sea lions spent little time at the operation, departing despite the continuing activity.

Most interaction events (53.9%) involved juvenile females; males were involved less (22.0%). Unsexed sea lions were involved in 24.2% of the interaction events. On three occasions, juvenile females preyed on the bait, something not observed for males.

Most sightings were of solitary animals (75.6%). Sightings of small groups ( $<5$ ) were common, whereas groups of 5 and 12 were only observed on one occasion each. In 78.6% of the cases of active predation on the longlines (interaction events), a single sea lion was involved, 15.7% of the cases involved two animals, and 2.9% of the interaction events involved groups of three or four. The larger groups (5 and 12 animals) did not appear to interact with the fishing operation and were only passing by and/or swimming around the operation area (“sightings without interaction”).

Although sightings and interaction events tended to decrease as the distance between the fishing operation and the rookery increased, there were no significant differences among the three distance ranges from Liliaguapi Island ( $p = 0.33$ ).

Most sea lion bites consisted of tearing of the body of the hake (67.1%), and fewer attacks focused on the viscera (32.9%). There



**Figure 4.** Variations in the number of (a) sightings, and (b) interaction events recorded during the fishing events throughout the study period.

was no significant relationship between the type of bite and AHCL ( $p > 0.05$ ).

### Losses of southern hake to spiny dogfish

Southern hake losses through predation by spiny dogfish were observed in 21 fishing events (45.8% of all fishing events), and represented 3.3% of the total catch of southern hake (by number). A maximum of 65 hake were preyed on by spiny dogfish per fishing event. On average, 4.6 hake (s.d. 12.1) were preyed on or damaged per fishing event. A seasonal interaction pattern was observed between fishing and spiny dogfish predation, with less loss of southern hake in summer. Predation was greater during the rest of the year, with small variations among fishing events (Figure 3c). The catch losses caused by spiny dogfish predation increased along with the AHCL (Table 2).

The average extent of spiny dogfish predation on adult southern hake per fishing event was greater than that on juveniles throughout the study period, except in June, when predation on juveniles was greater (Figure 3c). It should be pointed out, however, that only one fishing event was observed in June and that only one juvenile hake was preyed on by spiny dogfish then. The preference of spiny dogfish for adult hake during the whole year was confirmed by the Chesson Selectivity Index ( $\alpha$ ; Table 3).

The forward stepwise linear regression relating spiny dogfish to the duration of the gear in the water and the number of hooks set showed that each variable contributed significantly to the model (Table 2). The two variables related to fishing effort were not significantly correlated between each other ( $r = 0.17$ ,  $p = 0.4$ ).

Although spiny dogfish predation was slightly greater during fishing events using longlines with retained fishing systems as opposed to those with hand-held guides, the differences were not statistically significant ( $t = -1.56$ ,  $p = 0.14$ ).

## Discussion

### Sea lion predation on southern hake

Sea lion predation on southern hake caught on longlines was observed in 58% of the fishing events. However, despite this high interaction frequency, just 1.6% of the total number of southern hake caught was lost in this way. The figure corresponds to 227 kg using an average of 2.06 kg per southern hake, as determined from information collected during the 48 fishing events.

Our estimates of the number of interactions between sea lions and the fishery are lower than previous estimates for this species. Sepúlveda *et al.* (2007) reported average losses of 3.8–6.5% of the biomass caught in several artisanal fisheries off Chile; these values fall within the lower end of those found for sea lion interactions with fisheries off Uruguay, where Szteren and Páez (2002) estimated losses of 2–18%. Our results show that sea lions in the area studied do not currently cause significant loss of artisanal catches. Other factors that need to be taken into account when evaluating variations in artisanal yields are changes in the abundance of southern hake produced by natural causes or overfishing, changes in the availability of southern hake in the study area, oceanographic variability, fishing techniques, and the skill of fishers.

There are two main caveats to our estimates of losses of southern hake attributable to sea lion predation. Our analysis did not consider hake preyed on completely, i.e. those taken but leaving no evidence on the fishing gear. Nor did it consider losses attributable to the removal of pieces of the longline by sea

lion tugging. Indeed, portions of longline were lost in 21% of the fishing events observed, amounting to a total of 380 hooks. If every hook lost had caught a southern hake, then the total losses potentially caused by the sea lions would account for 6.8% of the total catch. However, it seems more likely that the pieces of longline lost had a similar efficiency to the parts recovered, so 17.5% of those would have caught southern hake, implying that the loss would have been 2.6% of the catch. Therefore, it is likely that our results slightly underestimated the real rates of predation.

In terms of hake being preyed on totally, Wickens *et al.* (1992) defined operational consumption as the notion that each sea lion could take its complete daily food requirement from the fishing gear. Following that criterion, and considering a hypothetical maximum predation scenario, sea lion predation on southern hake caught by longline rises to 3.5% (by number). This estimate assumes that the sea lions have a daily requirement equivalent to 4% of body weight (Kastelein *et al.*, 1995). The resulting figure of 3.5% of losses attributable to sea lion predation is close to the values obtained by Sepúlveda *et al.* (2007) and Szteren and Páez (2002). This analysis supports our opinion that interaction between the artisanal southern hake fishery and the South American sea lion is not great in the study area.

Although sea lions have been reported to be generalist and opportunistic predators whose diet is conditioned by the resources available to them (Aguayo and Maturana, 1973), dietary studies in different areas show a wide diversity of feeding behaviour (George-Nascimento *et al.*, 1985; Thompson *et al.*, 1998; Hückstädt *et al.*, 2007). Our results reveal trophic selection by age class on the southern hake available hanging on the longline, with a clear preference for the largest hake, regardless of their availability. By considering predation in relation to prey availability on the longline, we excluded other factors associated with free-swimming prey, such as speed, escape capability, and depth distribution. Therefore, we hypothesize that predation on the adult hake hanging on the longline represents a small expenditure of energy for the sea lion's daily food requirement, allowing the sea lions to sustain themselves on fewer fish.

The damage that the sea lion caused on the catches during fishing was not significantly associated with the availability of the fish caught or retained on the gear (Table 2). The lack of an association can be explained by the feeding and diving behaviour of sea lions, which naturally take largely pelagic prey (Hückstädt *et al.*, 2007) and dive mainly between 10 and 60 m (Werner and Campagna, 1995; Thompson *et al.*, 1998; Campagna *et al.*, 2001). The longlines used in the southern hake fishery keep the catch at 150–300 m, much deeper than the typical vertical feeding range of the sea lion. This also explains the lack of association between sea lion predation and fishing effort (the time the longline is in the water, the number of hooks; Table 2).

The frequency of interaction events in relation to the recorded loss of catches to sea lions suggests that predation rate per sea lion was not high. This is confirmed by the high percentage of sightings (57.3%), in which sea lions simply passed by or swam around rather than preying on the hake. Moreover, in most interaction events (75.3%), sea lions remained around the fishing operation for <10 min, and the reaction of the fishers was not a determining factor in them leaving the area. There was no clear relationship between age or sex class of sea lions and the extent of interaction with the southern hake fishery. Although it was often difficult to identify age and sex classes during fishing events, attacks by

males clearly did not dominate. In contrast, it is known that sea lion attacks on farmed fish are made mostly by adult and subadult males (Pemberton and Shaughnessy, 1993; Sepúlveda and Oliva, 2005).

The number of sea lions observed around the fishing operation during fishing events with recorded interactions varied between one and four animals; in 78.6% of the cases, the interaction was with solitary sea lions. Placing longlines at relatively inaccessible depths maintains a low availability of prey to the sea lions, promoting largely solitary feeding behaviour. These results on sea lion numbers around the fishing gear agreed with those of Sepúlveda *et al.* (2007) off Chile (4.7 animals) and by Szteren and Páez (2002) off Uruguay (1–4 animals). However, Hückstädt and Antezana (2003) recorded much larger numbers (up to 50 sea lions) during industrial fishing operations off central Chile; this can be explained by the large number of potential prey concentrated within a purse-seine during those operations (Hückstädt and Antezana, 2003).

Losses were observed during the retrieval phase, when the availability of the southern hake increased at shallower depths. Moreover, we observed sea lions approaching the fishing site immediately after seabirds began feeding on the waste from the evisceration of catches by the fishers. Such behaviour results in sea lions staying close to the vessel until the catches are retrieved by the fishers, making the fish more easily accessible to predation.

There was no significant trend of increasing numbers of sightings and interaction events when the distance between the fishing operation and the rookery decreased, suggesting that other factors influence the diet and feeding sites of sea lions (e.g. the availability of natural prey). This coincides with previous statements on the extent of interaction between sea lions and other fisheries or fish farms, and the relationship with distance from the nearest haul-out site (e.g. Hückstädt and Antezana, 2003; Sepúlveda and Oliva, 2005; Sepúlveda *et al.*, 2007).

We observed seasonal variation in the level of interaction between sea lions and artisanal fishing, with a minimum in summer in our study area. Such seasonal variation is likely to be related to changes in the abundance of sea lions in the study area attributable to the circannual rhythm of the species, conditioned principally by its reproductive activity (Sepúlveda *et al.*, 2001). During their reproductive period in summer, the sea lions move towards the breeding colonies where they concentrate and remain until the reproductive activity ends (Campagna and LeBoeuf, 1988). The breeding colonies nearest the study area are at Metalqui, Doña Sebastiana Island, and Guafo Island, where numbers reach 12 677, 9414, and 4822 sea lions, respectively (Oporto *et al.*, 1999). These three breeding colonies are located >100 km away from the study area, and as much as 250 km for Guafo Island.

Finally, we observed some fishers attempting to kill or injure sea lions by shooting at them during fishing events. However, owing to the mobility of the sea lions, the instability of the boat, and the distance between them, no cases of severe injury or death were recorded.

### Spiny dogfish predation on southern hake

Spiny dogfish preyed on the southern hake catches in fewer fishing events than sea lions; however, the attacks resulted in greater (3.3%) losses from the hake catch. As for sea lions, predation by spiny dogfish on southern hake was least in summer when the environmental availability and catches of hake peaked (Céspedes

*et al.*, 1996; Rubilar *et al.*, 1999), suggesting the displacement of these sharks far from the study area, possibly in association with reproductive behaviour. Although detailed information on the biology and ecology of the spiny dogfish in the eastern South Pacific is practically non-existent, research on the reproductive behaviour of spiny dogfish in New Zealand has revealed seasonal displacement between coastal and deeper water, with a greater oceanic influence determined by the periods of birth, mating, and ovulation (Graham, 1956; Hanchet, 1988).

The losses in hake catch attributable to spiny dogfish predation increased concomitantly with the availability of hake on the longlines. Sharks can detect prey at great distances based on their olfactory capability (Hobson, 1963; Tester, 1963), suggesting that, in addition to the hake itself, the bait used could also attract the dogfish. Independently of adult and juvenile hake availability on the longline, spiny dogfish preferred to prey on larger hake year-round.

### Implications for management

Demands for hunting permits to reduce the South American sea lion population by several unions of Chilean artisanal fishers require careful consideration of the extent to which sea lions interact with the different fisheries, spatially and seasonally. Moreover, more-quantitative information on the ecological role of the South American sea lion in coastal ecosystems is essential for decision-making on the subject around Chile. Considering (i) the many factors involved in the interaction between sea lions and artisanal fishing for southern hake, (ii) the limited understanding of the trophic web in the Patagonian ecosystem, (iii) the complex non-linear interactions within an ecosystem, and (iv) the capacity of pinnipeds to modify the structure and dynamics of the ecosystem as top predators, perhaps any attempt to reduce the sea lion population by hunting would not only fail to provide important benefits to fishers but could also produce ecological damage, at both population and ecosystem levels.

In the specific case of the southern hake in the study area within Chilean Patagonian fjords, the limited predation observed in our study reflects the necessity to evaluate other factors that may well have a greater effect on the economic situation of artisanal fishers, including resource scarcity as a consequence of overfishing, catches lost to other predators, competition with industrial fisheries, and the continuing decrease in the ex-vessel price of hake recently (by some 4% annually). Our results show that, at least for the study area, the level of interaction between the South American sea lion and the southern hake fishery currently does not require any type of measure to reduce the population size of the sea lion.

### Acknowledgements

We thank the artisanal fishers of Comau Fjord and Gulf of Ancud, who allowed us to conduct our observations on board their vessels, F. Goyeneche, J. Werner, L. Bedriñana, and R. Rojas, who participated as observers on many of the trips, and J. Uribe for valued help in the field. We are also grateful for the support and constructive comments from L. Osman during the planning of the research, to S. Pantoja for his valuable comments on an earlier version of the manuscript, to J. Soto for graphic support, to R. Veas for statistical analysis, and to C. Bustamante for taxonomic identification. RAQ was funded by the Programa de Investigación Marina de Excelencia (PIMEX-Nueva Aldea) of the Universidad de Concepción, which is financed by Celulosa Arauco y Constitución SA. ADIT was funded

by a MAE Scholarship from the Agencia Española de Cooperación Internacional (AECI) and by PIMEX-Nueva Aldea. Additional support for the research was provided by Fundación Pumalín. The manuscript was vastly improved by comments from and grammatical correction by the editors, Peter Shaughnessy, and two anonymous referees.

## References

- Aguayo, A., and Maturana, R. 1973. Presencia del lobo marino común (*Otaria flavescens*) en el litoral chileno. *Biología Pesquera*, 6: 49–75.
- Aguayo-Lobo, A., Díaz, H., Yáñez, J., Palma, F., and Sepúlveda, M. 1998. Censo poblacional del lobo marino común en el litoral de la V a IX Regiones. Informe Técnico Fondo de Investigación Pesquera FIP-IT/ 96-51. Ministerio de Economía, Chile.
- Baraff, L. S., and Loughlin, T. R. 2000. Trends and potential interactions between pinnipeds and fisheries of New England and the US west coast. *Marine Fisheries Review*, 62: 1–39.
- Bartheld, J. L., Pavés, H., Contreras, F., Vera, C., Manque, C., Miranda, D., Sepúlveda, D., et al. 2008. Cuantificación poblacional de lobos marinos en el litoral de la I a la IV Región. Informe Técnico Fondo de Investigación Pesquera FIP 2006-50. Ministerio de Economía, Chile.
- Beverton, R. 1985. Analysis of marine mammal–fisheries interactions. *In* *Marine Mammals and Fisheries*, pp. 3–33. Ed. by J. Beddington, R. Beverton, and D. Lavigne. George Allen and Unwin, London.
- Campagna, C., and LeBoeuf, B. J. 1988. Reproductive behaviour of southern sealions. *Behaviour*, 104: 233–261.
- Campagna, C., Werner, R., Karesh, W., Marin, M., Koontz, F., Cook, R., and Koontz, C. 2001. Movements and location at sea of South American sea lions (*Otaria flavescens*). *Journal of Zoology*, 255: 205–220.
- Céspedes, R., Adasme, V., Reyes, H., Braun, M., Figueroa, E., Valenzuela, V., Ojeda, V., et al. 1996. Identificación de áreas de reclutamiento de merluza del sur en la zona sur austral. Informe Técnico Fondo de Investigación Pesquera FIP-IT/93-20. Ministerio de Economía, Chile.
- Chesson, J. 1978. Measuring preference in selective predation. *Ecology*, 59: 211–215.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology*, 64: 1297–1304.
- Fertl, D. 2002. Interference with fisheries. *In* *Encyclopedia of Marine Mammals*, pp. 438–442. Ed. by W. F. Perrin, B. Würsig, and J. G. M. Thewissen. Academic Press, New York.
- Fordham, S., Fowler, S. L., Coelho, R., Goldman, K. J., and Francis, M. 2006. *Squalus acanthias* (South America subpopulation). IUCN Red List of Threatened Species, 2006.
- George-Nascimento, M., Bustamante, R., and Oyarzún, C. 1985. Feeding ecology of the South American sea lion *Otaria flavescens*: food contents and food selectivity. *Marine Ecology Progress Series*, 21: 135–143.
- Gómez, D., Bustamante, C., and Lamilla, J. 2007. Situación de *Squalus acanthias* Linnaeus, 1758 en el sur de Chile. Proceedings of the XXVII Congreso de Ciencias del Mar, Universidad Arturo Prat, Iquique, Chile.
- Graham, D. H. 1956. *A Treasury of New Zealand Fishes*. Reed, Wellington. 424 pp.
- Hanchet, S. 1988. Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 22: 537–549.
- Harwood, J. 1987. Competition between seals and fisheries. *Science Progress*, 71: 429–437.
- Hobson, E. S. 1963. Feeding behavior in three species of sharks. *Pacific Science*, 17: 171–194.
- Hückstädt, L. A., and Antezana, T. 2003. Behaviour of the southern sea lion (*Otaria flavescens*) and consumption of the catch during purse-seining for jack mackerel (*Trachurus symmetricus*) off central Chile. *ICES Journal of Marine Science*, 60: 1–9.
- Hückstädt, L. A., Rojas, C. P., and Antezana, T. 2007. Stable isotope analysis reveals pelagic foraging by the southern sea lion in central Chile. *Journal of Experimental Marine Biology and Ecology*, 347: 123–133.
- Kastelein, R., Kershaw, J., Berghout, E., and Wiepkema, P. 1995. The food consumption of South American sea lions (*Otaria flavescens*). *Aquatic Mammals*, 21: 43–53.
- Kauppinen, T., Siira, A., and Suuronen, P. 2005. Temporal and regional patterns in seal-induced catch and gear damage in the coastal trap-net fishery in the northern Baltic Sea: effect of netting material on damage. *Fisheries Research*, 73: 99–109.
- Lamilla, J., Acuña, E., Araya, M., Oliva, M., Kong, I., Villaroel, J. C., Hernández, S., et al. 2005. Lineamientos básicos para desarrollar el Plan de Acción Nacional de Tiburones. Informe Final Proyecto F.I.P. N° 2004-18. Ministerio de Economía, Chile. 223 pp. +7 Annexes.
- Lowry, L. F. 1982. Documentation and assessment of marine mammal–fishery interactions in the Bering Sea. *In* *Wildlife Nature Resources Conference*, Portland, Oregon, pp. 300–311. Ed. by K. Sobel. Transactions of the North American Wildlife Management Institute, 47.
- Netter, J., Kutner, M. H., Nachtsheim, C. J., and Wasserman, W. 1996. *Applied Linear Statistical Models*. Irwin, Chicago.
- Northridge, S. 1985. World review of interactions between marine mammals and fisheries. *FAO Fisheries Technical Paper*, 251.
- Oliva, D., Sielfeld, W., Buscaglia, M., Matamala, M., Moraga, R., Pavés, H., Pérez, M. J., et al. 2008. Plan de acción para disminuir y mitigar los efectos de las interacciones del lobo marino común (*Otaria flavescens*) con las actividades de pesca y acuicultura de la X y XI Región. Informe Técnico Fondo de Investigación Pesquera FIP 2006-34. Ministerio de Economía, Chile.
- Oliva, D., Sielfeld, W., Durán, L. R., Sepúlveda, M., Pérez, M. J., Rodríguez, L., Stotz, W., et al. 2003. Interferencia de mamíferos marinos con actividades pesqueras y de acuicultura. Informe Técnico Fondo de Investigación Pesquera FIP 2003-32. Ministerio de Economía, Chile.
- Oporto, J., Brieva, L., Navarro, R., and Turner, A. 1999. Cuantificación poblacional de lobos marinos en el litoral de la X y XI Regiones. Informe Técnico Fondo de Investigación Pesquera FIP-IT/97-44. Ministerio de Economía, Chile.
- Pemberton, D., and Shaughnessy, P. D. 1993. Interaction between seals and marine fish-farms in Tasmania, and management of the problem. *Aquatic Freshwater Ecosystems*, 3: 149–158.
- Rubilar, P., Céspedes, V., Ojeda, V., Cerna, F., Ojeda, G., Adarme, L., and Cuevas, A. 1999. Análisis de la estructura y condición biológica de los recursos merluza del sur y congrio dorado en aguas interiores de la X, XI y XII Regiones. Informe Técnico Fondo de Investigación Pesquera FIP-IT/98-02. Ministerio de Economía, Chile.
- Seco Pon, J. P., and Gandini, P. A. 2007. Bycatch of the piked dogfish *Squalus acanthias* Linné, 1758 (Chondrichthyes, Squalidae) in semi-pelagic longline fisheries at the Patagonian shelf. *Investigaciones Marinas*, 35: 85–88.
- Sepúlveda, M., and Oliva, D. 2005. Interactions between South American sea lions *Otaria flavescens* (Shaw) and salmon farms in southern Chile. *Aquaculture Research*, 36: 1062–1068.
- Sepúlveda, M., Oliva, D., and Palma, F. 2001. Daily and annual circarhythms activity in the South American sea lion *Otaria flavescens* (Carnivora: Otariidae) at the central zone of Chile. *Revista de Biología Marina y Oceanografía*, 36: 181–187.
- Sepúlveda, M., Pérez, M. J., Sielfeld, W., Oliva, D., Durán, L. R., Rodríguez, L., Araos, V., et al. 2007. Operational interaction between South American sea lions *Otaria flavescens* and artisanal (small-scale) fishing in Chile: results from interview surveys and on-board observations. *Fisheries Research*, 83: 332–340.

- Shima, M., Hollowed, A. B., and Van Blaricom, G. R. 2000. Response of pinniped populations to direct harvest, climate variability, and commercial fishery activity: a comparative analysis. *Reviews in Fisheries Science*, 8: 89–124.
- Sielfeld, W. 1983. *Mamíferos Marinos de Chile*. Ediciones de la Universidad de Chile, Santiago.
- Sielfeld, W., Guerra, C., Durán, L. R., Acuña, E., Aguayo, A., Sepúlveda, M., Palma, F., *et al.* 1997. Monitoreo de la pesquería y censo del lobo marino común en el litoral de la I–IV Regiones. Informe Técnico Fondo de Investigación Pesquera FIP-IT/95-28. Ministerio de Economía, Chile.
- Szteren, D., and Páez, E. 2002. Predation by southern sea lions (*Otaria flavescens*) on artisanal fishing catches in Uruguay. *Marine and Freshwater Research*, 53: 1161–1167.
- Tester, A. L. 1963. The role of olfaction in shark predation. *Pacific Science*, 17: 145–170.
- Thompson, D., Duck, C. D., McConnell, B. J., and Garrett, J. 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. *Journal of Zoology*, 246: 135–146.
- Torres, D., Yañez, J., and Cattán, P. 1979. Mamíferos marinos de Chile: antecedentes y situación actual. *Biología Pesquera*, 11: 49–81.
- Venegas, C., Gibbons, J., Aguayo, A., Sielfeld, W., Acevedo, J., Amado, N., Capella, J., *et al.* 2001. Informe Final Proyecto FIP 2000-22. Cuantificación Poblacional de Lobos Marinos en la XII Región. Fondo de Investigación Pesquera, Valparaíso. Ministerio de Economía, Chile. 92 pp.
- Werner, R., and Campagna, C. 1995. Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia. *Canadian Journal of Zoology*, 73: 1975–1982.
- Wickens, P. 1995. A review of operational interactions between pinnipeds and fisheries. *FAO Fisheries Technical Paper*, 346.
- Wickens, P. A., Japp, D. W., Shelton, P. A., Kriel, F., Goosen, P. C., Rose, B., Augustyn, C. J., *et al.* 1992. Seals and fisheries in South Africa—competition and conflict. *South African Journal of Marine Science*, 12: 773–789.
- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., *et al.* 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314: 787–790.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th edn, pp. 616–618. Prentice-Hall, Inc., Upper Saddle River, NJ.

doi:10.1093/icesjms/fsp235