

# The influence of wave exposure on the foraging activity of marine otter, *Lontra felina* (Molina, 1782) (Carnivora: Mustelidae) in northern Chile

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**Abstract** The marine otter *Lontra felina* has been said to prefer wave-exposed habitats over more protected sites in response to a greater prey abundance in exposed habitat. We examined how the foraging activity of *L. felina* is affected by the regime of wave exposure and prey availability at Isla Choros, northern Chile. Through focal sampling we recorded time spent by otters in foraging, the duration of dives, and the hunting success on a wave-exposed and a wave-protected site on the island. In addition, we quantified the abundance of prey in both habitats. Marine otters spent more time foraging in the wave-protected site compared with the wave-exposed habitat. Successful dives reached 26.9% in the wave-exposed habitats, and 38.2% in the wave-protected habitat. Foraging dives were 18% shorter in wave-exposed as compared with wave-protected habitat. Numerically, available prey did not differ significantly with habitat. Our results are more consistent with the hypothesis that wave-exposed habitats represent a sub-optimal habitat to foraging

marine otters. Marine otters' use of wave-exposed patches through northern and central Chile coastal areas probably reflects a low availability of suitable protected areas and greater human disturbance of more protected habitat.

**Keywords** Chile · *Lontra* · Marine otter · Foraging success · Dive time

## Introduction

The Chilean marine otter *Lontra felina* (Molina 1782), commonly known as “chungungo”, inhabits the Pacific coast, from northern Perú to Cape Horn and Isla de Los Estados (Sielfeld and Castilla 1999). *L. felina* is said to use coastal areas from 30 m in land to 150 m offshore (Sielfeld and Castilla 1999). On land, *L. felina* makes use of steep rocky shores where larger-sized rocks and deep crevices are present (Sielfeld 1983, 1990; Ebensperger and Castilla 1992). These habitat features seem to facilitate an imperceptible entrance into the water, and provide adequate conditions for the establishment of dens. Since steep rocky areas are typically associated with wave-exposed coastal places (Ebensperger and Castilla 1992), *L. felina* is frequently linked to this habitat. Indeed, surveys based on the presence of otter dens indicate that marine otters restrict their activity to wave-exposed areas with the presence of kelps such as *Durvillaea antarctica*, avoiding less-wave-exposed areas, protected habitats (Sielfeld 1983, 1990). A seemingly more frequent use of wave-exposed patches has been hypothesized to reflect greater patch quality in terms of prey abundance

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(Ebensperger and Castilla 1992; Ebensperger and Botto-Mahan 1997). Patch use theory indeed predict consumers should concentrate on more-productive habitats (Stephens and Krebs 1986).

For consumers that use diving to obtain their prey, optimal foraging models predict how long a diver should spend on the surface, the depth at which to forage, and the time under water in order to maximize foraging efficiency (e.g., Houston and Carbone 1992). According to these considerations, time foraging under water (i.e., diving time) should increase with depth (i.e., travel time), decrease with energetic costs of diving, but not vary with patch quality (Houston and Carbone 1992; Carbone and Houston 1994; Mori et al. 2002; Halsey et al. 2003). In addition, diving success is expected to increase with prey abundance, a measure of patch quality (Thompson and Fedak 2001).

We used these expectations from optimality to examine the behavior of a scarcely known dive forager, the marine otter *L. felina*. Specifically, we examined the hypothesis according to which a more frequent use of wave-exposed habitats by these otters represents an optimal strategy where wave-exposed patches indeed represent higher-quality habitat than wave-protected patches. Thus, and provided that depths are comparable between both habitat, we predicted dive time of chungungos not to vary with habitat irrespective of prey abundance. However, we expected otters to exhibit more successful dives when foraging in the wave-exposed, presumably better-quality, habitat. Alternatively, we considered the possibility that marine otters' use of wave-exposed habitats does not reflect an optimal choice. Compared to wave-exposed habitat (coastal areas exposed to dominant wave action), wave-protected patches (bays and places protected from dominant wave action) would provide marine otters with better physical conditions while foraging. Thus, a more frequent use of wave-exposed habitats might result from limited opportunities to use protected patches. If so, we predicted that otters would exhibit shorter and less successful dives in wave-exposed patches.

We recorded the behavior of an insular population of *L. felina* while foraging in both wave-exposed and wave-protected patches. We contrasted the foraging frequency, diving time, and hunting success between both habitats. We complemented these observations with estimates of prey availability known to be consumed by *L. felina* in the study area, Villegas (2002) in wave-exposed and wave-protected habitats, and related these data to the foraging activity of otters in both habitats.

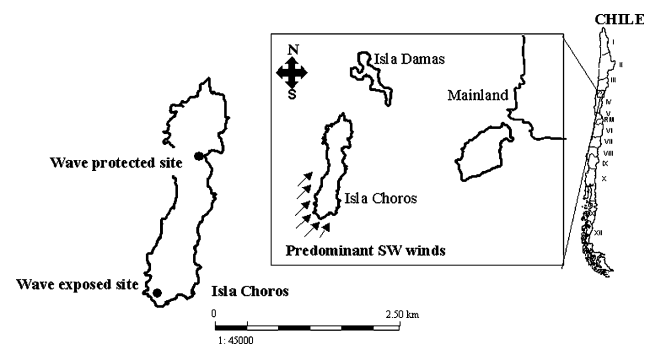
## Materials and methods

### Study area

The study took place at Isla Choros (29°15'S, 71°32'W), northern Chile. Our study was based on 28 days of observations similarly spaced between January and December 2001. Isla Choros is a 4 by 0.4 km island located about 8 km from the mainland and being part of the Humboldt Penguin National Reserve (Simeone et al. 2003). The island has no permanent human inhabitants, but occasional fishermen exploit the subtidal fringe. The climate is arid with periodic fogs and rain during winter months. The island is oriented from north—south. Since the predominant wind direction is southwest, the west coast of the island is more wave-exposed than the east coast, which is more wave-protected (Fig. 1). The wave-exposed side is characterized by steep and craggy zones with abundant surf water on the surface, the product of water motion due the strong action of waves. In contrast, the wave-protected coast side was characterized by relatively calm bays, without surf waves and less water motion (Fig. 2). The range of water depth (3–15 m) was similar in both sites. During each sampling event, both habitat were sampled simultaneously.

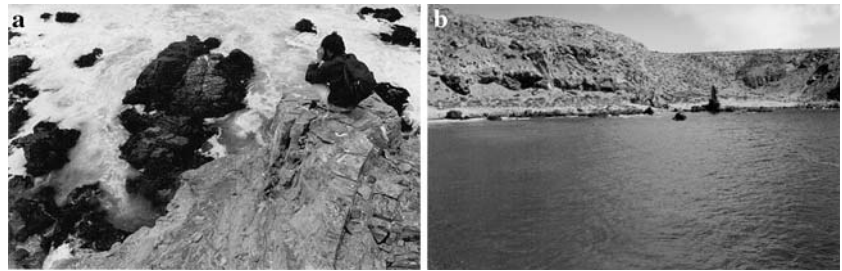
### Diving time and hunting success

The complete perimeter of the island was surveyed and two main vantage points were selected: one on the exposed and one on the protected coastal sides of the island (Figs. 1, 2). We chose these points based on the presence of favorable conditions for dens, and on the direct observation of otter's foraging activity (Ostfeld et al. 1989; Ebensperger and Castilla 1992; Sielfeld and Castilla 1999). Vantage points were



**Fig. 1** Geographical location and orientation of Isla Choros, and location of vantage points (black dots) used to record the activity of *Lontra felina*. Arrows indicate predominant wind direction

**Fig. 2** Representative views of the **a** wave-exposed, and **b** wave-protected coast sides of Isla Choros, northern Chile



atop cliffs 10–30 m above sea level and provided unobstructed view along the shoreline. Daily observations began nearly 1 h after dawn and ended about a half hour before dusk. During our focal animal sampling, one observer (MJV) undertook continuous observation as soon as an otter was sighted, and stopped when the otter left the field of view. Since the observer was within 30–60 m of the subject, observations were aided by the use of  $7 \times 50$  binoculars. Because the predominant behaviour of otters was foraging, we were able to keep a continuous record of time underwater (dive time), and whether a foraging time was successful (prey obtained) or not. Our observations were based on unmarked subjects, but based on simultaneous observations of two or more individuals in the same site, and from differences in pelage color and marks, we were certain that our wave-exposed site was used by 4–6 different individuals; at least 2–3 different otters visited the wave-protected site. The rather small number of individuals observed simply reflects the endangered status of *L. felina* according to the International Union for Conservation of Nature and Natural Resources (IUCN 2004).

#### Prey abundance

We quantified the abundance of prey known to be consumed by *L. felina* in our study site (Villegas 2002) to estimate the overall productivity of both patches examined. We did so by means of five 50-m-long transects on each side of the island. Subtidal transects were separated by 50–70 m from each other and their location coincided with where otters were regularly seen hunting. Along each transect, an observer by means of hooka diving recorded all potential prey in each of five equally spaced stations; depth of water at the stations ranged from 3 to 15 m, which matched the observed depths of otters when foraging. We recorded all individual fish over a 5-min sweeping of a 5-m radius circular area; crustaceans and mollusks observed near the bottom were quantified with  $1 \text{ m}^2$  quadrants.

#### Statistical analysis

We carried out statistical analyses with Statistica 6.0 for Windows (StatSoft Inc., Tulsa, Oklahoma). Throughout, we utilized nonparametric statistics, except when assessing the simultaneous influence of habitat and success of prey capture on diving time. In such case, we followed Zar (1996) and used the squared-root transformation to equalize variances whenever they were correlated with their means. When comparing percent time spent foraging and foraging success across habitats, we used one-tailed tests based on our a priori predictions: we were expecting otters to exhibit longer and more successful dives in the more-exposed habitat. Throughout we report data as mean  $\pm$  SD.

## Results

#### Diving time and hunting success

A total of 53 focal observations were recorded in both sites. Duration of focal observations averaged  $13.7 \pm 11.5$  min ( $n = 53$ ). Overall, otters spent  $40.5 \pm 38.9\%$  of their activity time foraging. Other activities such as resting, grooming, sunning and playing accounted for the remaining activity time. *L. felina* spent 31% ( $\pm 34\%$ ,  $n = 28$ ) of their time foraging in the wave-exposed site, while they spent 51% ( $\pm 42\%$ ,  $n = 25$ ) of their activity time to foraging in the wave-protected site, a statistically significant difference (Mann–Whitney  $U$  test,  $Z_{\text{adj}} = 1.88$ ,  $P = 0.030$ ).

We observed a total of 235 foraging dives. Successful dives reached 26.9% in the wave-exposed habitat ( $n = 78$ ), and 38.2% in the wave-protected habitat ( $n = 157$ ), a statistically significant difference (two-ratio difference test,  $P = 0.048$ ). While the analysis of variations (ANOVA) revealed that foraging dives by marine otters were 18% shorter in the wave-exposed as compared with the wave-protected habitat irrespective of hunting success (one-way ANOVA on squared-root

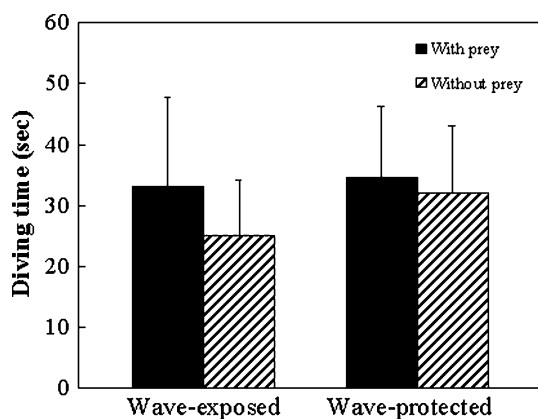
of sec,  $F_{1,231} = 7.30$ ,  $P = 0.0074$ ), most of this effect was driven by unsuccessful dive (Fig. 3). The analysis also revealed that foraging dives were 14% shorter when they were unsuccessful irrespective of habitat ( $F_{1,231} = 8.69$ ,  $P = 0.0035$ ).

### Prey availability

A total of 13 fish, 11 crustacean, and seven mollusk species were recorded during the subtidal sampling in both habitats of Isla Choros (Table 1). Crustaceans were numerically the most important prey available in the wave-exposed habitat, followed by mollusks and fish, which were equally abundant (Bonferroni-corrected Kruskal–Wallis test,  $H_{2,92} = 9.50$ ,  $P = 0.0087$ ; Table 2). Crustaceans were also the most common prey available in the wave-protected habitat, but similarly abundant to mollusks (Bonferroni-corrected Kruskal–Wallis test,  $H_{2,92} = 12.99$ ,  $P = 0.0015$ ). When habitats were compared, fish were significantly more abundant in the wave-protected habitat while crustaceans were more abundant in the wave-exposed habitat (Table 2). If all potential prey are pooled, the total number of prey potentially available to otters did not differ statistically between the two habitats (Mann–Whitney  $U$  test,  $Z_{adj} = 0.96$ ,  $P = 0.336$ ; Table 2).

### Discussion

Based on the presence of feces and dens on land, *L. felina* is said to prefer wave-exposed habitats over more wave-protected areas of the coast (Sielfeld 1983, 1990; Ebensperger and Castilla 1992), and this greater use of wave-exposed habitats is suggested to mirror



**Fig. 3** Untransformed diving time (s) of *Lontra felina* recorded in focal sampling of animals successful or not in the catch of prey, in wave-exposed and -protected habitat in Isla Choros, northern Chile. Values are means  $\pm$  SD

differences in the availability of prey taken by *L. felina* (Ebensperger and Castilla 1992). Thus, marine otters are hypothesized to use wave-exposed sites more because these patches provide more abundant food. Optimality considerations, on the other hand, predict that diving time should increase with depth (a surrogate of travel time), decrease with energetic costs of diving, but vary little with patch quality (Houston and Carbone 1992; Carbone and Houston 1994; Mori et al. 2002; Halsey et al. 2003). Besides, diving success is expected to increase with prey abundance, a measure of patch quality (Thompson and Fedak 2001). Therefore, while we predicted dive time of marine otters not to vary with food quality in the habitat, otters should exhibit more successful dives when foraging in the wave-exposed, presumably a better-quality habitat. Alternatively, if wave-exposed habitats represent a

**Table 1** Abundance (in  $m^{-2}$ ) of potential prey of *Lontra felina* in both wave-protected and wave-exposed habitats at Isla Choros, northern Chile

Species	Wave-protected	Wave-exposed
Fishes		
<i>Aplodactylus punctatus</i>	0.013 $\pm$ 0.016	0.005 $\pm$ 0.014
<i>Cheilodactylus variegatus</i>	0.010 $\pm$ 0.013	0.001 $\pm$ 0.003
<i>Chromis crusma</i>	0.031 $\pm$ 0.106	0.004 $\pm$ 0.011
<i>Girella laevisfrons</i>	0.004 $\pm$ 0.011	
<i>Isacia conceptionis</i>	0.015 $\pm$ 0.031	0.025 $\pm$ 0.051
<i>Labrisomus philippii</i>	0.001 $\pm$ 0.003	
<i>Mugiloides chilensis</i>	0.013 $\pm$ 0.016	0.004 $\pm$ 0.011
<i>Paralabrax humeralis</i>	0.001 $\pm$ 0.002	
<i>Paralichthys</i> sp.	0.001 $\pm$ 0.003	
<i>Prolatilus jugularis</i>	0.001 $\pm$ 0.005	
<i>Scartichthys viridis</i>	0.002 $\pm$ 0.008	0.001 $\pm$ 0.003
<i>Sebastes capensis</i>	0.001 $\pm$ 0.003	
<i>Trachurus murphyi</i>	0.020 $\pm$ 0.071	
Crustaceans		
<i>Betaeus</i> sp.	1.778 $\pm$ 5.333	40.000 $\pm$ 40.200
<i>Cancer setosus</i>	0.006 $\pm$ 0.003	0.001 $\pm$ 0.002
<i>Cyclograpsus cinereus</i>	9.778 $\pm$ 11.155	28.444 $\pm$ 79.510
<i>Homalaspis plana</i>	0.004 $\pm$ 0.002	0.160 $\pm$ 0.800
<i>Leptograpsus variegatus</i>	0.010 $\pm$ 0.001	0.889 $\pm$ 2.667
<i>Paraxantus barbiger</i>	0.160 $\pm$ 0.800	4.444 $\pm$ 7.055
<i>Petrolisthes</i> sp.	5.333 $\pm$ 6.928	258.667 $\pm$ 124.515
<i>Petrolisthes desmarestii</i>	0.160 $\pm$ 0.800	0.480 $\pm$ 1.327
<i>Petrolisthes violaceus</i>	21.333 $\pm$ 28.844	71.111 $\pm$ 107.439
<i>Rhynchocinetes typus</i>	5.760 $\pm$ 13.966	10.720 $\pm$ 26.400
<i>Taliepus dentatus</i>	0.160 $\pm$ 0.800	1.600 $\pm$ 3.055
Mollusks		
<i>Calyptrea trochiformis</i>		1.576 $\pm$ 5.093
<i>Concholepas concholepas</i>	0.480 $\pm$ 1.759	0.640 $\pm$ 2.215
<i>Chiton</i> sp.		0.889 $\pm$ 2.667
<i>Chiton cumingi</i>	1.778 $\pm$ 5.333	5.333 $\pm$ 8.944
<i>Fissurella cumingi</i>	1.778 $\pm$ 3.528	0.320 $\pm$ 1.600
<i>Tegula atra</i>		1.600 $\pm$ 8.000
<i>Tegula tridentata</i>	9.600 $\pm$ 40.464	

Data on abundance are mean  $\pm$  SD. The number of replicates for each value of abundance is 35 (five sampling stations per each of five transect plus two intertidal quadrants per transect)

**Table 2** Abundance (ind m<sup>-2</sup>) of main prey of *Lontra felina* in wave-protected and wave-exposed habitats at Isla Choros, northern Chile

Prey category	Wave-protected	Wave-exposed	Between-habitat contrast ( <i>P</i> -value)
Fishes	0.111 ± 0.161 <sup>a</sup>	0.039 ± 0.059 <sup>a</sup>	0.0014
Crustaceans	14.706 ± 28.535 <sup>b</sup>	116.824 ± 187.637 <sup>b</sup>	0.0167
Mollusks	11.882 ± 39.665 <sup>b</sup>	5.212 ± 10.319 <sup>a</sup>	0.4307
Pooled	9.750 ± 29.874	45.054 ± 125.944	0.3361

Data are mean ± SD. The number of replicates for each value of abundance is 35 (five sampling stations per each of five transect plus two intertidal quadrants per transect). Contrasts between habitat for each prey category were assessed by means of Bonferroni-corrected Mann–Whitney *U* tests (critical  $\alpha$ -value set at 0.017). Letters in superscript indicate statistical differences among prey categories within each habitat, after using a Bonferroni-corrected Kruskal–Wallis test

sub-optimal habitat to foraging otters, we predicted these carnivores to exhibit shorter and less successful dives in wave-exposed patches.

Our data provided little support for the expected differences in habitat quality. Total abundance of prey was statistically similar in the wave-exposed and wave-protected patches studied. Crustaceans were more abundant in the wave-exposed habitat, but fish were more abundant at the wave-protected site. Under these conditions, marine otters spent less time foraging and were less successful at catching prey in the wave-exposed habitat. Since *L. felina* at Isla Choros preys mostly on crustaceans and secondarily, on fish (Villegas 2002), marine otters seemed inefficient foragers when diving at the wave-exposed habitat. Moreover, otters exhibited shorter dives in wave-exposed patches. Taken together, these findings are consistent with the hypothesis that wave-exposed habitats represent a sub-optimal habitat to foraging marine otters.

It could be argued that otters still might be efficient foragers through selecting large sized, more profitable prey while foraging in the wave-exposed habitat. However, populations of *L. felina* from southern Chile do not select prey on the basis of total energy content (Medina et al. 2004). In addition, otters from Isla Choros (Villegas 2002) and other southern and northern Chile localities (Ostfeld et al. 1989; Medina 1995) consistently consume small to medium-sized fish and crabs, but less so larger prey. We suggest that the presumably low foraging efficiency of *L. felina* when in wave-exposed habitat may be linked to a higher cost of swimming and diving in these patches (Ebensperger and Botto-Mahan 1997). Visual cues seem important to foraging otters (Gentry and Peterson 1967), and so the relatively high turbulence of water in wave-exposed patches may interfere more with location of bottom-dwelling prey. Water turbulence may also interfere directly with swimming performance by increasing the energetic cost of transport. Thus, underwater condi-

tions of wave-protected areas may provide better conditions for longer dives, which might result in greater hunting success. Alternatively, abundance of prey may not adequately reflect prey availability in both habitats. The more secretive habits of crabs and shrimps (more abundant in the wave-exposed habitat) may determine overtly low prey availability in this habitat compared with fish, a more abundant prey in the wave-protected habitat. Either way, our data imply that a more frequent use of wave-exposed habitat by northern Chile populations of *L. felina* is the result of limited opportunities to use more protected patches.

Wave-protected coastal areas tend not to have the large rocks and deep crevices used by otters on land to establish dens (Sielfeld 1983; Ebensperger and Castilla 1992). Thus we hypothesize that otters use wave-exposed habitat because shores on this habitat provide adequate den conditions nearby. In fact, habitat conditions at Isla Choros are exceptional in that both wave-exposed and wave-protected habitats provide conditions for dens (Villegas 2002), and correspondingly, otters foraged in both. Additionally, however, wave-protected sites may be visited more frequently by local fishermen, which in turn may disturb otters in this preferred habitat with their presence. Thus, both the availability of adequate physical conditions for dens and differences in human disturbance may drive otters to use wave-exposed sites more frequently. Further studies are needed not only to confirm our results, but to expand them through quantifying direct habitat use (with and without human presence), and energetic profitability attained by individual otters when foraging under different regimes of water turbulence and depth, two factors influencing diving costs.

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## References

- Carbone C, Houston AI (1994) Patterns in the diving behaviour of the pochard, *Aythya ferina*: a test of an optimality model. *Anim Behav* 48:457–465
- Castilla JC, Bahamondes I (1979) Observaciones conductuales y ecológicas sobre *L. felina* (Molina) 1782 (Carnívora: Mustelidae) en la zona central y centro norte de Chile. *Arch Biol Med Exper (Chile)* 12:119–132
- Ebensperger LA, Castilla JC (1992) Selección de hábitat en tierra por la nutria marina, *Lutra felina*, en Isla Pan de Azúcar, Chile. *Rev Chil Hist Nat* 65:429–434
- Ebensperger LA, Botton-Mahan C (1997) Use of habitat, size of prey, and food-niche relationships of two sympatric otters in southernmost Chile. *J Mammal* 78:222–227
- Gentry RL, Peterson RS (1967) Underwater vision of the sea otter. *Nature* 216:435–436
- Halsey L, Woakes A, Butler P (2003) Testing optimal foraging models for air-breathing divers. *Anim Behav* 65:641–653
- Houston AI, Carbone C (1992) The optimal allocation of time during the diving cycle. *Behav Ecol* 3:255–265
- International Union for Conservation of Nature and Natural Resources (2004) Red list of threatened species. URL: <http://www.redlist.org/>
- Medina G (1995) Feeding habits of marine otter (*Lutra felina*) in southern Chile. In: Reuther C, Rowe-Rowe CD (eds) *Proceedings of the VI International Otter Colloquium, Pietermaritzburg, Hankensbüttel*, pp 65–68
- Medina G, Delgado-Rodríguez C, Alvarez RE, Bartheld JL (2004) Feeding ecology of the marine otter (*Lutra felina*) in a rocky seashore of the south of Chile. *Mar Mammal Sci* 20:134–144
- Mori Y, Takahashi A, Mehlum F, Watanuki Y (2002) An application of optimal diving models to diving behaviour of Brünnich's guillemots. *Anim Behav* 64:739–745
- Ostfeld RS, Ebensperger L, Klostermann LL, Castilla JC (1989) Foraging, activity budget, and social behavior of the South American marine otter *Lutra felina* (Molina 1782). *Nat Geogr Res* 5:422–438
- Sielfeld W (1983) *Mamíferos marinos de Chile*. Ediciones de la Universidad de Chile, Santiago
- Sielfeld W (1990) Características del hábitat de *Lutra felina* (Molina) y *L. provocax* Thomas (Carnívora, Mustelidae) en Fuego-Patagonia. *Investigaciones Científicas y Tecnológicas, Serie Ciencias del Mar (Chile)* 1:30–36
- Sielfeld W, Castilla JC (1999) Estado de conservación y conocimiento de las nutrias en Chile. *Est Oceanol (Chile)* 18:69–79
- Simeone A, Luna-Jorquera G, Bernal M, Garthe S, Sepúlveda F, Villablanca R, Ellenberg U, Contreras M, Muñoz J, Ponce T (2003) Breeding distribution and abundance of seabirds in islands off north-central Chile. *Rev Chil Hist Nat* 76:323–333
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton
- Thompson D, Fedak MA (2001) How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim Behav* 61:287–296
- Villegas M (2002) Utilización de hábitat por parte de *Lontra felina* (Carnívora; Mustelidae) en Isla Choros (IV Región, Chile), en relación a la abundancia y distribución de sus presas. Facultad de Ciencias del Mar, Marine Biology thesis, Universidad Católica del Norte, Coquimbo, Chile, p 62
- Zar JH (1996) *Biostatistical analysis*, 3rd edn. Prentice Hall, Upper Saddle River