

Predation by killer whales (*Orcinus orca*) on southern right whales (*Eubalaena australis*) off Patagonia, Argentina: effects on behavior and habitat choice

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ABSTRACT

Predation can be a strong selective force affecting the social traits and habitat choice of prey species. Killer whales or orcas (*Orcinus orca*) and southern right whales (*Eubalaena australis*) coexist in the waters off Península Valdés, Argentina. Over the last three decades, right whales have changed their distribution along the Peninsula by abandoning the area with the highest occurrence of orcas and moving into two adjacent bays. Between 1972 and 2000, 117 orca – right whale encounters were observed. From 112 encounters, 63 (56.3%; mean duration \bar{x} =12.3 min) involved no apparent changes in the behavior of either species; in 37 encounters (33%; \bar{x} =27.6 min) obvious behavioral changes were seen; and in 12 encounters (10.7%; \bar{x} =81.1 min) actual attacks were observed. The orca / right whale ratio was maximum (1.8 orcas per right whale) in actual attacks, and minimum (1.3 orcas per right whale) in the other two categories. Most encounters (90.6%) occurred along the Eastern Outer Coast of the Peninsula. Here, the overall number of encounters decreased with time, from 68 in 1972-1980, to 26 in 1981-1990, to 23 in 1991-2000. However, while encounters decreased along the Eastern Outer Coast they increased in other areas. Orcas may assess right whale group size and their own group size before approaching and attacking. During encounters, right whales showed behaviors (active calf protection, use of tail as a weapon, use of shallow waters, increased group size, rosette formation) that could be adaptive to decrease predation success. The aggregation of right whales on nursery grounds such as Península Valdés has been proposed to be an adaptation to reduce individual predation risk. The abandonment of the Eastern Outer Coast by right whales has lowered the number of encounters with orcas with a subsequent decrease in the attack rate over time. At present it is not possible to determine whether predation pressure *caused* the change in habitat use by right whales in Valdés. However, our data suggest that the ‘predation hypothesis’ could partly explain the shift of southern right whales into the bays.

KEY WORDS: KILLER WHALES, SOUTHERN RIGHT WHALES, PREDATION, HABITAT, MIGRATION, ATLANTIC OCEAN

INTRODUCTION

Predation pressure has been recognized as a strong selective force for prey species (Lima and Dill, 1990; Deecke et al., 2002). Killer whales or orcas (*Orcinus orca*) are a primary predator of marine mammals. Orcas have been observed attacking at least 20 species of cetaceans, 14 species of pinnipeds, the sea otter and the dugong (Jefferson et al., 1991). Encounters of orcas with baleen whales have been recorded for a number of species, including the blue whale (Tarcy, 1979), the fin whale (Heide-Jorgensen, 1988), the humpback whale (Whitehead and Glass, 1985; Flórez-González et al., 1994), the gray whale (Baldrige,

1972; Goley and Straley, 1994; Ternullo and Black, 2002; Mizrock and Rice, 2006), Bryde's whale (Silber et al., 1990), the minke whale (Guinet et al., 2000; Mizrock and Rice, 2006) and the bowhead whale (Mitchel and Reeves, 1982).

Interactions of orcas with southern right whales (*Eubalaena australis*) have been recorded in all of the main nursery grounds of this species throughout the Southern hemisphere, with the possible exception of New Zealand (Sorensen, 1950; Jefferson et al., 1991; Visser, 1999). In South Africa and Argentina orcas have been seen to encircle and harass right whales but apparently not kill them (Donnelly, 1967; Cummings et al., 1972).

The orcas of Península Valdés, Argentina have been studied since 1975 and the population has remained stable at an estimated 30 individuals (López and López, 1985; Bubas, 2001; Iñíguez, 2001). The Valdés orcas are known for their habit of stranding intentionally on beaches to prey upon South American sea lions (*Otaria flavescens*) and southern elephant seals (*Mirounga leonina*) (López and López, 1985; Hoelzel, 1991; Iñíguez, 2001; Iñíguez et al., 2002). Changes in the seasonal distribution of one orca group have been described by Iñíguez (2001) as associated to changes in the spatial distribution of southern elephants seals at Península Valdés. This orca group was frequently seen in this area before 1985.

The right whale population of Península Valdés has been studied since 1970 (Payne, 1986). Its female breeding population size was estimated at 92 individuals in 1971, 328 in 1990 (Cooke et al., 2001), and 547 in 1997 (IWC, 1998). During the austral winter and spring southern right whales use Valdés as a nursery ground (Payne, 1986). Orcas and right whales coexist in the same waters at Valdés for about six months each year. However, because of the relative difficulty of seeing predation events in the wild, observations of encounters between the two species are scarce. The first reported attack of orcas on right whales at Valdés dates to 1971 (Cummings et al., 1972).

The spatial distribution of right whales around Península Valdés has changed since the 1970's (Rowntree et al., 2001). The Eastern Outer Coast (EOC) of the Península was an important nursery area for right whales in the 1970's (Rowntree et al., 2001). At the time, the EOC had the highest concentration of females with calves (Payne, 1986). In the 1980's right whales abandoned the EOC and gradually moved to Golfo Nuevo (GN) and Golfo San José (GSJ). By the 1990's GN had the highest proportion of females with calves and few whales were seen along the EOC (Rowntree et al., 2001), a pattern that has continued to the present.

Researchers have debated the role of orca predation on the behavioral ecology and migratory patterns of baleen whales (Corkeron and Connor, 1999; Clapham, 2001; Connor and Corkeron, 2001). The 'predation hypothesis' (Corkeron and Connor, 1999) suggests that a reduction in predation risk on baleen whale calves from the relatively abundant orcas in high latitudes provides the primary fitness benefit to females which migrate to lower latitudes to give birth. Baleen whale calves, and yearlings in their first migration, appear to be particularly vulnerable to large predators (Sumich and Harvey, 1986; Clapham, 2000; Ternullo and Black, 2002). Clapham (2001) argues that the role of orca predation on the social ecology of species like the humpback whale appears to be minimal, and that the risk of orca predation is not strong enough to explain baleen whale migrations. Other authors (Jefferson et al., 1991; Pitman et al., 2001) claim that orcas may play a more important role as a predator of marine mammals than is commonly suspected.

In this paper we propose that if orca predation is an important evolutionary force acting on right whales, then right whales should exhibit behaviors that have evolved to reduce predation risk. Also, we suggest that the relatively higher occurrence of orcas along the EOC may have driven right whales to abandon the EOC and move into GN and GSJ where the risk of orca predation appears to be less.

Corkeron and Connor (1999) proposed between-site and between-population comparisons of orca predation rates on right whales in the southern hemisphere as a natural 'field test' of the predation hypothesis. Here we report 117 observations of orca – right whale encounters over a period of 29 years at Valdés. We hope that future comparisons with other populations will help test this hypothesis worldwide.

MATERIALS AND METHODS

Study site

Right whales and orcas coexist along the shores of Península Valdés (PV), Argentina (42°S, 63°W), and the Southern tip of Río Negro (RN) Province. The Península is a large cape which encloses two bays: Golfo San José (GSJ) to the north and Golfo Nuevo (GN) to the south, and a section of shoreline facing the open South Atlantic – the Eastern Outer Coast (EOC) (Fig. 1). The coast of the two bays alternates between

regions of broad beaches with gradually sloping sandy or pebbled bottoms and harder bottoms littered with blocks of material that have fallen from the cliffs that rim the edges of both bays in many places. Right whales at Valdés tend to be distributed close to shore along the 5 m depth contour, where they linger longest over smooth, sandy or pebbled bottoms (Payne, 1986). The cliffs provide an exceptional setting to observe the whales from shore without any apparent disturbance to their behavior.

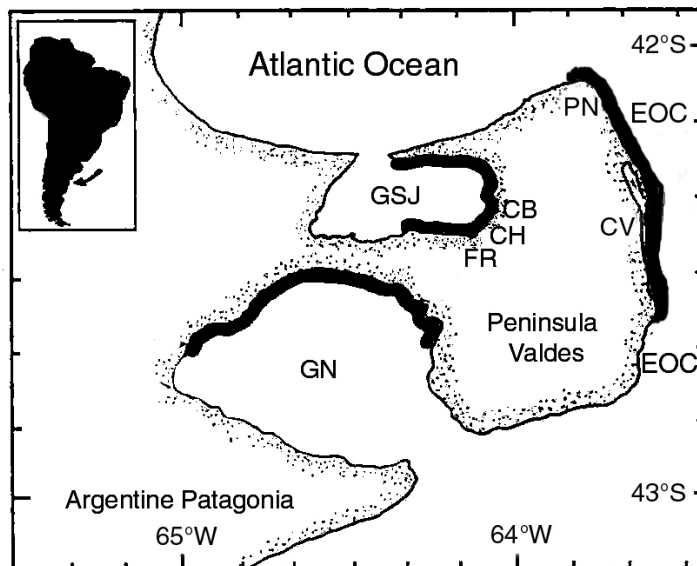


Figure 1. Map of Península Valdés showing the sites and the three areas where most encounters were observed. CB: Camp Bay; CH: Cliff Hut; CV: Caleta Valdés; FR: Fracaso; GN: Golfo Nuevo; GSJ: Golfo San José; EOC: Eastern Outer Coast; PN: Punta Norte. Shading indicates the regions of concentration of right whales over the study period (map modified from Rowntree et al., 2001)

Data collection and analysis

The term “encounter” refers to the simultaneous occurrence of orcas and right whales at the same site (at distances ranging from 1.5 km to physical contact between the two species), whether or not behavioral changes in either species were observed (Jefferson et al., 1991). Because of the unpredictability of the encounters, observations were made *ad libitum* (Altmann, 1974; Mann, 1999). Field notes from all observers were processed and summarized. All data were collated and standardized to calculate descriptive statistics. The variables recorded included date, time, site, duration of the encounter, number of orcas and right whales present, distance between them, and descriptions of their behavior. However, the information available for each encounter was not always complete and consistent with the observations made during other encounters. For this reason, not all observations were used in all the analyses, and the sample sizes (and degrees of freedom) vary among tests. In many cases, the encounters had already started when the observers began to record data, so the average durations we present underestimate actual durations.

Most encounters were observed by the authors, and a few encounters were reported by other experienced and reliable observers such as park rangers and naturalist tour guides. The vast majority were land-based observations from beaches and cliffs using binoculars and spotting scopes. In a few cases animals were observed from boats or from an aircraft. Photographs were taken whenever possible.

Encounters were recorded over a period of 29 years (1972-2000). During the periods 1975-1982 and 1995-2000 some of the authors (JCL, RB) lived on the shores of the EOC year round and made systematic observations of orcas and recorded their encounters with right whales. Other authors (GH, RP, MS) lived on the shores of GSJ year round or during extended periods of time from August through November while studying right whales during the peak of their calving season. They also kept records of orca – right whale encounters. As a consequence, sampling effort (and chances of observing encounters) was similar and most intense on the EOC and in GSJ in those years during the time of right whale peak abundance. Therefore, we used data from the EOC and GSJ collected in 1975-1982 and 1995-2000 to compare the spatial and temporal distribution of interspecific encounters. In Río Negro (RN) we made observations only during the 1990’s.

We divided encounters into three categories along a gradient of increasing activity and intensity of encounters. Encounters labeled Grade 1 were characterized by the simultaneous observation of orcas and right whales in the same area (with a separation of up to 1.5 km between the two species), with no direct physical contact between the species and no apparent changes in their behavior. In Grade 2 encounters, orcas and right whales were in close proximity with potential physical contact. We observed behavioral changes and higher levels of activity in both species, but no bites, blood or other evidence of a real attack. Grade 3 encounters were considered actual attacks. They were characterized by high levels of activity of both species, and by bites from the orcas on a right whale’s body, or by blood or pieces of blubber visible at the water surface. Some of the “case studies” described below include particularly detailed behavioral observations.

Statistical tests were carried out using JMP version 7 for Windows (SAS Institute Inc. 2007). Tests were two-tailed and the results were considered to be significant at $P < 0.05$.

RESULTS

Group size and composition

We observed 117 orca – right whale encounters between 1972 and 2000. At least 445 orcas and 291 right whales were involved in these encounters (though there are certainly multiple observations of the same orcas, some observations of right whales may also include multiple observations of the same individual). The mean number of orcas per encounter ($\bar{x}=3.8$; $SD=2.12$) was significantly higher than the mean number of right whales ($\bar{x}=2.5$; $SD=2.44$) ($t=-4.87$; $df=115$; $p<0.001$), with a mean ratio of 1.5 ($SD=1.9$) orcas per right whale in 116 encounters with known number of individuals. Right whales considered to be in the same group when they were separated by an approximate distance of five “whale lengths” (or approximately 75 m) or less.

Of 112 encounters that could be graded, 63 (56.3%) were classified as grade 1, 37 (33%) as grade 2, and 12 (10.7%) as grade 3. The mean estimated distance between orcas and right whales in grade 1 encounters was 252 m ($SD=405$). In all other encounters there was potential or actual physical contact between the two species. The duration of 79 graded encounters was recorded. The mean duration increased significantly along the gradient of intensity (one-way ANOVA, $F_{(2,76)}=12.34$, $p<0.001$) and was maximum during attacks (Table 1).

The average number of right whales per encounter (2.5) did not vary along the gradient (Fig. 2). However, the average number of orcas increased with intensity of encounters from 3.3 orcas in grade 1 to 4.5 orcas in grade 3 encounters. As a result, the orca / right whale ratio was minimum in grade 1 encounters (1.3 orcas / right whale) and maximum in grade 3 encounters (1.8 orcas / right whale). This difference is significant ($t=-2.12$; $df=72$; $p=0.038$).

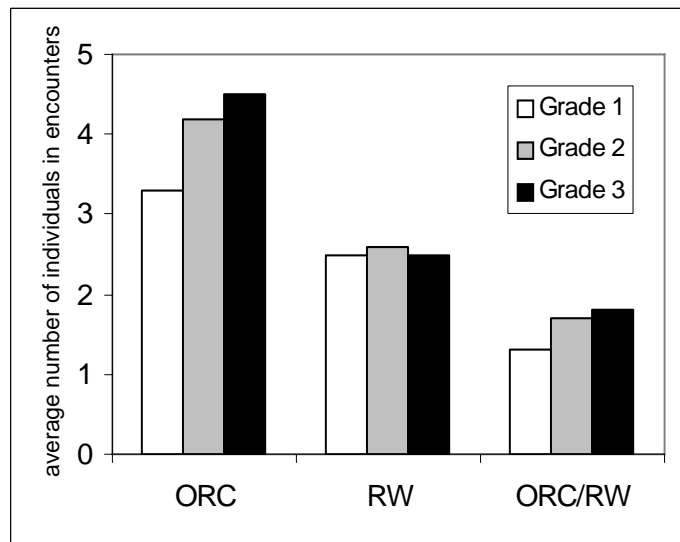


Figure 2. Average number in graded encounters of orcas (ORC), right whales (RW), and the ratio of orcas to right whales (ORC/RW).

The age composition of groups was different for both species. For right whales, adults were the most frequent age class observed during the encounters (Table 1). Almost two thirds (64.3% or 187 whales) of the right whales observed in encounters were adults, and they were the only age class present in 72 (61.5%) encounters, including seven of the 12 attacks. Right whale calves were seen in six grade 1 encounters, nine grade 2 encounters, two grade 3 encounters and in two encounters that were not graded (because of missing details in the field notes), totalling 28 calves in 19 (16.2%) encounters. Juvenile right whales were recorded in 20 (17.1%) encounters. The age class of 23 (7.9%) right whales was not determined.

Adult orcas were present in the majority of encounters (Table 1). Adult male orcas were seen in 101 (86.3%) encounters, and they represented one third (33.5%) of all orcas observed. Adult females were seen in 62 (53%) encounters and represented at least 19.8% of all orcas. Ninety-two orca calves were present in 54 (46.2%) encounters, and juveniles were seen in 26 encounters (22.2%). The age and sex class of 70 (15.7%) orcas were not specified in the field notes analyzed.

Species	Age / sex	1	2	3	All
Orca	adult male	92.1	81.1	100	89.3
	adult female	52.4	59.5	58.3	55.4
	calf	46	51.4	50	48.2
	juvenile	14.3	29.7	50	23.2
Right whale	adult	79.4	75.7	75	77.7
	adult female	9.5	24.3	8.3	14.3
	calf	9.5	24.3	16.7	15.2
	juvenile	15.9	18.9	25	17.9
		12.3 (22)	27.6 (35.8)	81.1 (80.7)	27.7 (45)

Table 1. Percentage of encounters graded 1 to 3 (N=112) in which each age and sex class was recorded. The mean duration (and SD) of encounters (in min) is given in the last row.

During the 12 attacks (Grade 3), 30 right whales and 54 orcas were seen. Adult right whales (including mothers) represented 80% of the attacked whales (24 out of 30); they were observed in 10 (83.3%) attacks, and they were the only age class present in seven (58.3%) attacks. Right whale calves were seen in only two attacks (16.7%). Solitary right whales were attacked in six (50%) occasions: four were adults, one was a juvenile and one was a solitary calf. It could not be determined whether this solitary calf was separated from its mother by the orcas or whether it had already been weaned, although its small size suggested that it was not a yearling.

Adult male orcas participated in all of the 12 attacks and were the only orcas present in four of them. In contrast, they were present in 88.8% (87 out of 98) non-attack encounters. Of the eight known adult male orcas in this population, three of them were present in at least 75% of the attacks (the adult males in the remaining attacks were not identified). Three other adult males were never positively identified during orca encounters with right whales. Adult female orcas were recorded in 58.3% of attacks (7 out of 12) and juveniles were recorded 50% of attacks (6). Solitary orcas attacked on only two occasions: both animals were solitary adult males that attacked solitary right whales.

Behavioral aspects of the encounters

Some encounters were carefully timed by observers who also made detailed notes on the behavior of both species. The following “case studies” are the most representative summarized descriptions of grade 2 and grade 3 encounters, and will be used to discuss several aspects of the interactions. Case letter, observer, grade, site, area, date and time are given at the beginning of each description. Table 2 provides a summary of the behavioral patterns we observed in both species during 18 encounters for which we had detailed descriptions.

Case A. Obs.: RP. Grade 2. Camp Bay – Cliff Hut, GSJ, September 24, 1972, 1313hs. From an aircraft circling over the whales in GSJ, two adult orcas, one male and one female, were followed visually for three hours as they swam west past a line of eight right whale mother-calf (M/C) pairs strung out in at regular

intervals very near the shore. When within about 15 meters of each mother/calf pair the orcas gradually slowed to a stop where they remained for perhaps 20 seconds while each mother right whale made the same reaction to them—she flexed her tail stock laterally and held it there, as if cocked for a lateral slash. Once the mother was in this posture the orcas would turn slowly away and continue their original course. In one case, the orcas made a slight acceleration towards a calf that was on the orca's side of its mother's body. The calf responded by pressing its body firmly against its mother's, who had cocked her tail to one side then lashed her tail sideways at a moderate speed but without hitting either orca. Both right whales swam fast, staying in water so shallow a continuous track of mud was stirred up. The orcas stopped, remained motionless for perhaps 10 seconds, then turned slowly away and continued to the next mother/calf pair in a strikingly straight course—an indication that the orcas could determine the whales' position with great exactness. They soon joined a group of mothers with calves that had been closest to the Cliff Hut, where they could be studied by another observer (Katy Payne) who watched as several of the right whale females, all of which had been approached by the orcas, formed a circle in which their heads were directed toward the center (the "rosette" formation). While maintaining this formation, they thrashed the water with their flukes quite violently. They maintained this star-shaped formation and their energetic activity for about 40 min, while making loud snorts and blows that were audible in air. About an hour after the first sighting, two orca M/C pairs were spotted in the same area. Two orcas approached a right whale M/C pair in shallow water and subsequently left but approached them later two more times, until one of the adult right whales made a lateral slash with her tail and both orcas left, continuing to swim further from shore. After another lone orca was seen passing without incident by the head of another right whale mother, no further interactions were observed that day (see Payne, 1995, for further description).

Case B. Obs.: JCL. Grade 3. Punta Norte, EOC, September 28, 1975, 1630hs. About 45 min after catching a juvenile elephant seal by intentionally stranding and grabbing it, dragging it into the water, and feeding on it, a group of seven orcas (including one adult male) attacked a lone male juvenile right whale 40-50 m from shore. They bit its flanks, back, genital area and right fluke. As the right whale rolled repeatedly in an apparent effort to hit the orcas with its head, the orcas repeatedly bit its belly. At 1730 the orcas left the right whale but returned a few minutes later and attacked it again. While some of the orcas pushed the right whale into a deeper channel, the adult male orca patrolled the shoreline as if searching for potential seal prey or perhaps to prevent the right whale from reaching shallower waters. A black and white object approximately 30-40 cm long and 5-10 cm wide appeared floating on the surface close to the whale. The object matched the size and shape of a white lesion along the right whale's caudal peduncle that had not been seen before the attack. It appeared to be a slab of blubber and skin torn from the right whale by the orcas but not consumed by them. Petrels, gulls and cormorants pecked at the object. Visual contact was lost at dusk. At 1530 on September 29, the same group of orcas, the attacked juvenile right whale and seven adult right whales were seen at the same site. When the orcas were 100 m from the right whales, most of those adult right whales formed a "rosette" with tails out and heads toward the center. The orcas swam through this formation, splitting the group of right whales apart, and leaving the right whales to swim off in different directions. The orcas then moved toward the previously attacked juvenile right whale, which was now 20 m from shore next to another right whale. When the orcas approached, the other right whale fled, whereupon the previously attacked juvenile was pushed by the orcas and attacked it again on its front and sides. At 1610 the orcas left the area, returning at 1700 hours. They approached the same juvenile right whale but did not attack it. This time the orcas swam closer to shore and one of them attempted unsuccessfully to catch an elephant seal. At 1745 the orcas left and were not seen again that day. The attacked juvenile right whale swam slowly offshore and was not observed again in the area.

Case C. Obs.: CG. Grade 3. Camp Bay, GSJ, August 28, 1981, 1330hs. A lone adult right whale was seen striking the water surface vigorously and repeatedly with its tail and then swimming at high speed close to the shore of Camp Bay (GSJ), while an adult male orca kept pace with the right whale, and traveled parallel to its course, 30-40 m offshore of the right whale. Ten minutes later, the orca attacked the right whale, biting its right flank and holding on with its teeth for about 30 sec. Then the orca bit the right whale's jaw and maintained its bite for about 15 sec, while the orca rolled about its long axis--sometimes exposing its belly to the air. The orca then separated from the right whale before attacking again. When it did, it bit, and held on with its teeth four more times. While this was taking place, a kelp gull was seen pecking at the water around the whale as if it were feeding. After this, both whales moved out of sight behind a cliff. No right whale the size of the attacked animal was found dead at the site on the following days.

Case D. Obs.: GH. Grade 2. Fracaso Bay, GSJ, September 9, 1982, 1645hs. One adult male and at least five orcas of undetermined age were spotted in the same location where three right whales were swimming towards shore. Many sea birds were feeding near them. Suddenly, one right whale sped forward creating lots of turbulent water and a female orca surfaced behind it. A right whale calf was observed at the surface completely still. The orcas approached it several times and milled around it, but no definite evidence of an attack was seen. For logistic reasons, observations were stopped at this time. The next morning a right whale calf was found dead on Fracaso Beach, in the same bay where this incident was observed. On its body were orca tooth marks. Pieces of pectoral fins, tail flukes and skin were missing.

Case E. Obs.: CG. Grade 3. Caleta Valdés, EOC, October 30, 1988, 1130hs. Nine to 10 adult and juvenile orcas swam slowly to the South and approached a lone adult right whale traveling North along Caleta Valdés. The orcas encircled the whale, and the juveniles in the group attacked it on its flanks, pectoral fins and jaw, while the whale arched its back, made repeated lateral slashes with its tail, and changed its direction of travel to southward. The orcas followed for about 60 min, and attacked in threes and fours. Two adult right whales came from offshore and joined the attacked whale near the shore. The right whales formed a very compact group with close physical contact. They swam North, side by side, close to the shore, and each touched with its flipper the flipper of the whale next to it. At this point, the adult orcas left, leaving only the juveniles to follow the right whales, which they did for another 90 min. At 1400 the adult orcas rejoined the juveniles, swam between the juveniles and the right whales and led them South away from the right whales. The three right whales, continued moving North for the remaining 40 minutes that the observer could see them.

Case F. Obs.: EI. Grade 3. Río Negro, September 6, 1996, 1100hs. This encounter occurred in Punta Bermeja, a site North of Península Valdés that is part of the home range of the same orca population that visits the Peninsula (Iñíguez, 2001). Three adult male orcas seized a solitary adult right whale by its pectoral flippers apparently to prevent it from moving toward shallower water. The right whale emitted loud sounds that were audible in air and rolled actively at the surface. Three adult female orcas milled around the attack. The right whale hit one of the three female orcas with its tail, after which the female orca remained still for several minutes. Bites were seen on the pectoral fins, head and back of the right whale, and the water around it was bloody and oily. Two juvenile orcas kept at a distance of 700 to 800 m and did not participate in the attack, which lasted for over 150 min.

Case G. Obs.: RB. Grade 2. Punta Norte, EOC, September 14, 2000. A group of four adult female orcas, two juveniles and two calves patrolled the surf area at Punta Norte for about 60 min before approaching one adult right whale and a M/C pair. The two adult whales stayed parallel to each other near the coastal reef, keeping the calf in between and making repeated lateral slashes with their tails. During the encounter the orcas split into two groups and came back together several times: one group milled around the whales and the other moved about 100 m offshore where the members of the orca group slapped their tails on the water surface before returning toward the right whales. Ninety-five min later, two more adult right whales joined the whales that were being harassed, and formed a compact group with them, milling, arching their backs, keeping the calf in the center and staying at a distance of 20-80 m from the coastal reef, where water depth ranges between 10 and 20 m. After the orcas left the area, the whales stayed at the same site, actively swimming in circles without changing location.

Case H. Obs.: MS. Grade 2. Cliff Hut, GSJ, October 13, 2000, 1550hs. Two orcas, one of which was an adult male and the other was an adult female or a juvenile of indeterminate sex, were spotted about 400 m offshore, milling around a group of three adult right whales and a very small calf. Unusually intense splashes, flipper slapping and white water were seen. Muddy water surrounding the group indicated that the whales were in very shallow water (likely between 5 and 10m). One adult right whale kept actively pushing the calf with its head toward the center of the right whale group. At 1615, the body of an orca hurtled almost completely out of the water, followed by the tail of a right whale that was being swung in the same arc that the orca traveled along. This gave the impression that the orca had been struck a blow from the right whale's tail, hard enough to throw the orca into the air. About one min later, one of the orcas was seen at a distance of 100m, swimming away from the whales, while the other orca remained out of sight underwater. At 1620, both orcas were seen about 200 m from each other—both swimming away from the

group of right whales. At this point one of the adult right whales initiated an extremely fast pursuit of one of the orcas, but stopped at a distance from it of about 300m and slapped the water's surface with its flippers about 10 times. It then rolled and returned slowly back to the group of right whales while both orcas continued to swim away to the East, mostly underwater, and were not seen again that day. At 1630 a right whale M/C pair coming from the West joined the group. All whales stayed together in the same place and the adults were active at the surface, milling, rolling and slapping their flippers against the water. Five minutes later, two of the adults left this group, and the two M/C pairs remained close together for at least 45 minutes floating in very shallow water, keeping the calves between them. No other right whales were seen in the area. A flock of kelp gulls hovered over the group throughout the encounter, but they did not descend to pick up anything from the water, suggesting that no bits of blubber were dislodged from any whale. The conclusion, though tentative, is that this encounter was an example of right whales successfully driving off orcas by force, before these activities had resulted in significant bodily wounds to any participant.

Species	Behavior pattern	Grade 2	Grade 3	Study case
Right whale	use of shallow water	8	3	a B E g h
	tail slash	4	3	a C E g
	increase group size	3	2	a B E g h
	rosette formation	1 + 2?	1	a B g? h?
	flee from orcas	2	3	B C d E
	hit orca with tail	1 + 1?	1	F H?
	chase orca	1		H
Orca	differential roles among orcas	5	3	E F g
	milling around rw	7	1	d E g h
	bite on a rw's body		6	B C E F
	bite on a rw's head		5	B C E F
	pushes a rw with its head [?]	3	1	B
	bite on a rw's flukes or flippers		4	B E F
	approach and leave a rw	3		a d
split a rw group		1	B	

Table 2. Behavior patterns observed in grade 2 (N=8) and grade 3 (N=10) encounters. The figures are the number of encounters (Grade 2 and Grade 3) in which each pattern was observed. Study cases in CAPS are grade 3. A question mark (?) indicates that the behavior possibly occurred during the encounter but could not be confirmed. rw = right whale.

Spatial and temporal distribution of the encounters

Significantly more orca – right whale encounters (106 or 90.6%) were seen along the EOC than in all other areas ($\chi^2=268.7$; $df=3$; $p<0.001$) (Table 3). When the whole study period is considered (regardless of the observation effort), the number of recorded encounters per decade in all areas combined decreased with time, from 68 encounters (58.1% of all recorded encounters) in 1972-1980, to 26 (22.2%) in 1981-1990, to 23 (19.7%) in 1991-2000 ($\chi^2=32.46$; $df=2$; $p<0.001$) (Table 3).

However, the trend in each area is different, with a relative decrease in sightings along the EOC and an increase in the other areas when combined (Table 3). For example, in 1972-1980 virtually all encounters (98.5%) were observed along the EOC, with only 1.5% seen in GSJ. This changed during the 1990's: the percentage of encounters in the EOC dropped to 69.6% and it increased to 30.4% in all other areas combined (Table 3).

When only the two periods with the most intense and comparable observation effort are considered (periods when some of the authors lived at Península Valdés), this trend also holds. In 1975-1982, the EOC was the site of 97.8% of encounters, and only 2.2% occurred in GSJ; whereas in 1995-2000, 66.7% occurred at the EOC and 33.3% were recorded in GSJ, GN and RN ($\chi^2=27.89$; $df=3$; $p<0.001$) (Table 3).

Period	EOC	GSJ	GN	RN	Total
1972-1980	67 (98.5)	1 (1.5)	0	0	68
1981-1990	23 (88.5)	3 (11.5)	0	0	26
1991-2000	16 (69.6)	1 (4.3)	4 (17.4)	2 (8.7)	23
Total	106 (90.6)	5 (4.3)	4 (3.4)	2 (1.7)	117

Periods with similar sampling effort					
1975-1982	88 (97.8)	2 (2.2)	0	0	90
1995-2000	14 (66.7)	1 (4.8)	4 (19)	2 (9.5)	21
Total	102 (91.9)	3 (2.7)	4 (3.6)	2 (1.8)	111

Table 3. Number of orca – right whale encounters by area during the three decades of the study. The numbers between brackets are the percentage of encounters for each area over the total in the corresponding period. EOC: Eastern Outer Coast; GSJ: Golfo San José; GN: Golfo Nuevo; RN: Río Negro.

A comparison between the periods 1975-1982 and 1995-2000 in the two areas (EOC and GSJ) with the highest observation effort shows that orca/right whale encounters became less frequent with time. In the EOC the frequency decreased significantly from 11 encounters per year for the eight years 1975-1982 to 2.33 encounters per year for the six years 1995-2000 ($t=2.98$; $df=12$; $p=0.011$). In GSJ the change in frequency (from 0.25 to 0.17 encounters per year) over the these same two periods was not significant ($t=0.35$; $df=12$; $p=0.73$) (Fig. 3).

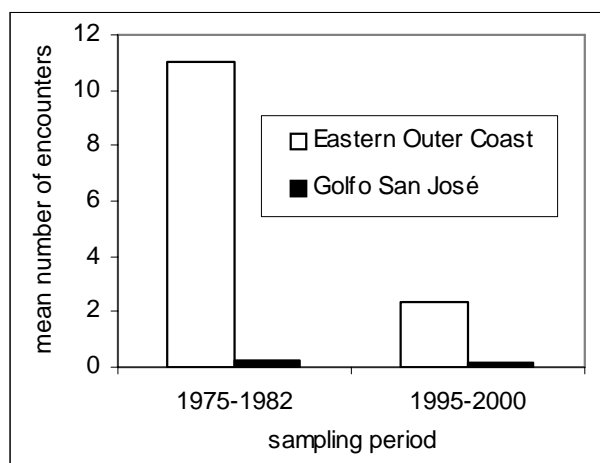


Figure 3. Mean number of encounters per year in the two sites and the two periods for which we had similar sampling effort.

During the 1996-2000 period there were on average 120 sightings of orcas per year off Valdés. The monthly rate of orca sightings along the EOC varied throughout the year and had two seasonal peaks that are clearly related to the higher abundance of sea lion and elephant seal pups (Fig. 4). The Sep - Nov peak in orca sightings (when orcas hunt for southern elephant seals) (López and López, 1985; Hoelzel, 1991; Iñíguez et al., 2002), also coincides with the time of highest right whale abundance in Valdés (Rowntree et al., 2001). As a consequence, the highest monthly rate of encounters between orcas and right whales occurred during those months. The monthly rate of encounters in EOC waters decreased between the periods 1975-1982 and 1995-2000. The highest monthly rate of encounters in 1975-1982 was 2.8 (in Oct), and in 1995-2000 it was 1.2 (in Nov)—a 57% reduction. Finally, in 1975-1982, the orca/right whale encounters occurred over eight months (May to Dec), whereas in 1996-2000 this “time window” of encounters was reduced to only four months (Aug to Nov) (Fig. 4).

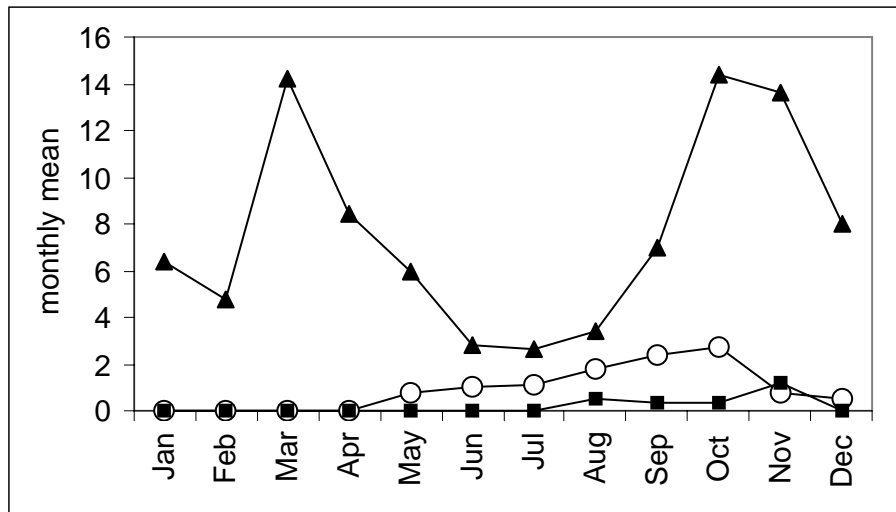


Figure 4. Mean monthly number of orca sightings in 1996-2000 (black triangles), and of orca - right whale encounters in 1975-1982 (open circles) and 1995-2000 (black squares) in the Eastern Outer Coast.

DISCUSSION

Group size and composition

Young or weak animals are more vulnerable to attacks by predators than healthy adults, and orcas would be expected to prefer the young as prey over the adults (Jefferson et al., 1991). However, right whale calves were not the main target of orca attacks in Península Valdés. In the 1970's right whale mother-calf pairs represented 68% of all identified whales in the EOC (Payne, 1986). Nevertheless, calves represented only 9.6% of all right whales observed in orca – right whale encounters. In contrast, adult right whales not accompanied by calves were the most frequent age category present, and the majority of confirmed attacks involved only adults. The presence of calves in a group of right whales is not a condition for orcas to attack. Furthermore, orcas are known to attack, kill and eat the previously considered “invincible” sperm whales in a group containing no calves (Pitman et al., 2001). It is possible that right whale calves were present in more attacks than observed. However, the attacks were relatively long (81 min on average) and it is unlikely that the observers did not see the calves, unless they were killed and sank before observations began.

Reports of orca attacks on large whales show no consistent pattern regarding the presence and the role of adult male orcas. They range from absence of adult males (Morejohn, 1968; Cummings et al, 1972; Vidal and Pechter, 1989) to presence with varying degrees of involvement (Tarcy, 1979; Arnborn et al., 1987; Silber et al., 1990) to active participation in the attacks (Whitehead and Glass, 1985; Flórez-González et al., 1994; Pitman et al., 2001). In Valdés, adult male orcas were present in 81% of grade 2 encounters (e.g., cases A and H), they were present in 100% of the attacks (e.g., cases C and F), and were the *only* orcas present in one third of them. Although more attacks should be witnessed to clarify the role of adult male orcas, the presence of at least one adult male appears to increase the likelihood of an attack. Of the eight identified adult male orcas in Valdés, three of them were present in the majority of the encounters, and three others were never positively identified in them. Individual differences in predator behavior of orcas in Valdés have been described (Hoelzel, 1991). Individual specialization within identified orca groups from Northern Patagonia showed that seasonal movements of two adult males were largely associated with the movement of South American sea lions, while a third adult male was associated more closely with southern elephant seal movements (Iñiguez 2001).

Orcas would be expected to reduce the risk of attacking the much larger right whales by increasing their own group size (Baird, 2000) or by attacking groups with fewer whales. In Valdés, the orca / right whale ratio increased with intensity of the encounters. Orca groups averaged 4.3 animals when attacking right whales, which is consistent with the most frequent group size of orcas (1 to 5) observed to harass or

prey upon large whales (except minke whales) (Jefferson et al., 1991). The same orcas in Valdés form smaller groups containing 2.1 (Iñíguez et al., 2005) to 3.2 individuals (López and López, 1985) on average while hunting for pinnipeds. The average orca group size off Northern Patagonia reported by Iñíguez et al. (2005) was 2.1. The reason for this relatively small group size may be that larger groups of orcas patrolling pinniped rookeries over multiple days may reduce prey capture rate. Longer patrolling periods and larger orca groups increase the pinnipeds' ability to recognize and avoid danger in Northern Patagonia (Iñíguez, 2001). Group size is affected by the prey type and size among several predator species, including hyenas, jackals and lions (Packer and Ruttan, 1988). We propose that orcas may "assess" their own group size and the group size and potential danger of their prey types at Península Valdés before actual attacks. This is consistent with the idea of "pre-selection" of particular prey species among social carnivores (Kruuk, 1972).

Behavioral aspects of the encounters: right whale behavior

Use of shallow water. Most mother-calf pairs in Valdés prefer water depths of around 5 m (Payne, 1986), a pattern similar to that found for right whales off South Africa (Best, 1990). Gray whales flee into shallow water at the approach of orcas (Morejohn, 1968), and cows occupy the innermost areas of the breeding lagoons possibly to reduce the risk of orca attacks on their calves (Swartz, 1986). Humpback whale cows on the nursery grounds also prefer areas with relatively calm, shallow water (Whitehead and Moore, 1982; Mattila and Clapham, 1988; Clapham and Mayo, 1987). In cases A and H (both included mother-calf pairs and no attack occurred), muddy water indicated extremely shallow depth. This strategy could make right whale cows more efficient than other whales at avoiding attacks. Other cetaceans in Valdés also swim close to shore to avoid orcas. Dusky dolphins swim in extremely shallow water when orcas are within 1 km, a behavior that possibly hides them from the orcas' echolocation and reduces the orcas' ability to maneuver (Würsig and Würsig, 1980).

Use of tail as weapon and rosette formation. Right whales can inflict serious damage to potential attackers by sweeping and slashing their enormous tails (Payne, 1995). Right whales were observed hitting orcas with their tails, which resulted in withdrawal by the orcas (cases F and possibly H). Humpback whales also thrash their tails when harassed by orcas (Whitehead and Glass, 1985; Flórez-González et al., 1994). The "rosette" formation observed as a response to orca attacks in right whales (cases A and B) has likely evolved as a defense against orca and shark attacks (Jefferson et al., 1991). Sperm whales also use this antipredator strategy (Pitman et al., 2001).

Increase group size and fleeing. Right whales grouped together during some encounters (cases E, G, H; also Cummings et al., 1972), as has been observed in gray (Ljungblad and Moore, 1983) and sperm whales (Arnbom et al., 1987). It is possible that right whales have evolved this strategy to decrease the risk of predation by exploiting the "confusion effect" (Landeau and Terborgh, 1986), or by combined defense (Inman and Krebs, 1987). Fleeing from orcas has also been observed in right whales (cases B, C, D) and in other cetaceans (Jefferson et al., 1991).

Behavioral aspects of the encounters: orca behavior

Appraising their prey. Orcas did not approach the nearby right whales in over one half of the encounters (those classified as grade 1). This sort of encounter is also the most typical between orcas and humpback whales in Alaska (Dolphin, 1987). However, in one third of the encounters in Valdés (grade 2), orcas approached and harassed right whales, but attacks were not observed (cases A, G, H). Orcas may "test" their prey to single out disabled, sick or old animals which could later be killed by a larger group acting cohesively (Whitehead and Glass, 1985; Jefferson et al., 1991; Constantine et al., 1998). Also, adult orcas could be teaching and training their young to hunt, as postulated for these and other orcas when hunting for pinnipeds (López and López, 1985; Hoelzel, 1991; Guinet, 1991; Iñíguez, 1993; Iñíguez et al., 2002). Juvenile orcas were present in one third and calves in one half of the grade 2 encounters, and both categories were present in one half of the attacks. Given the potential danger of attacking a much larger prey like the right whale, these speculations seem likely explanations of grade 2 encounters, during which adult orcas could also practice their hunting techniques (Baird, 2000).

Attack behavior and body parts preferred. When we observed bites during the attacks, orcas aimed at the lower jaw, flanks and pectoral fins of right whales. Several accounts of orca attacks on baleen whales

mention those body areas and the tongue as the most common parts eaten (e.g., Baldrige, 1972; Whitehead and Glass, 1985; Jefferson et al., 1991; Ternullo and Black, 2002). The most plausible reason for this selective strategy appears to be the avoidance of the whales' tail as a potential source of injury to the orcas (Silber et al., 1990). However, in case B a juvenile right whale was bitten on its right tail fluke and on its caudal peduncle during an attack.

Sex and age differences in attack behavior and cooperation. In case F adult male orcas seized a solitary adult right whale by its pectoral fins, apparently to prevent it from escaping into shallower water. This seemed to be a coordinated attack with segregation of roles by age and sex classes: adult male orcas grabbed, bit and charged at the right whale, females also charged but did not bite, and juveniles stayed at a distance. Case E also presents evidence of age-related behavioral differences, but it shows the opposite situation: juvenile orcas were the only attackers, although adults were also present. Similar accounts of synchronized activities and differential roles have been described for orca attacks on cetaceans (Jefferson et al., 1991; Flórez-González et al., 1994; Pitman et al., 2001) and pinnipeds (López and López, 1985; Hoelzel, 1991; Iñíguez, 2001) but the roles of each age and sex class are not always consistent among interactions. Regardless of the roles of individual orcas, cooperative hunting can be explained not only by the individual benefit gained but also by inclusive fitness, given that at least some of the orcas in Valdés are closely related (Hoelzel, 1991).

Spatial and temporal distribution of the encounters

The frequency of orca – right whale encounters observed in the EOC decreased between the 1970's and the 1990's. Because of low observation effort during most of the 1980's, we cannot speculate about what happened in those years. However, there is an obvious explanation for the decrease. Since the 1970's, right whales changed their distribution in Valdés during the calving season: they abandoned the EOC and moved into GN and GSJ (Rowntree et al., 2001). The EOC continues to be the area with the most orca sightings, probably because it supports the major pinniped colonies where orcas hunt (López and López, 1985; Hoelzel, 1991; Iñíguez, 2001). As a consequence, by abandoning the EOC right whales reduced their chances of encountering orcas. Interestingly, not only the monthly frequency of encounters decreased but also the time window during which encounters occurred in the EOC decreased from eight to four months per year (Fig. 4).

The reasons why right whales abandoned the EOC are less obvious. Rowntree et al. (2001) suggest that storms in the mid 1970's may have altered the bottom topography of the EOC, eliminating an eddy that was used as protection from strong water currents by right whales, who shifted further south and then abandoned the area completely. In South Africa, right whales also deserted some bays in favor of others as nursery areas for unknown reasons (Best, 1990). The seasonal distribution of orcas in Valdés is correlated to the distribution of pinnipeds (Iñíguez, 2001): orcas concentrate their hunting effort along the EOC where the capture rate of pinnipeds is greatest (Hoelzel, 1991; Iñíguez, 2001). Also, the EOC faces the open Atlantic ocean, has steep drop-offs and does not have shallow bays for right whales to protect themselves from orcas and from strong winds and storms. GSJ and GN have such sites and also have calmer water. If a 'relatively lower predation risk is sufficient to favor migration' (as proposed by Connor and Corkeron, 2001) over long distances, then we propose that it should also be sufficient to promote the abandonment of the EOC by right whales in favor of the nearby GSJ and GN where encounters with orcas are relatively less frequent and where they may occur over a shorter period of time each year. The abandonment of the EOC and the establishment of a new nursery area in GN had no apparent negative effect on the growth rate of the right whale population (Cooke et al., 2001; Rowntree et al., 2001).

There is no clear evidence that predation pressure on right whales along the EOC intensified since the 1970's. The orca population size appears stable at no more than 30 individuals (López and López, 1985; Bubas, 2001; Iñíguez, 2001), and the right whale population is increasing (IWC, 1998; Cooke et al., 2001). However, there is some indication of a potential decrease in predation risk with time at least in GSJ. Würsig and Würsig (1980) reported 21 orca sightings over 26 months (0.8 sightings/month) for the period 1973-1976 in GSJ. In contrast, in 1995-2000 we saw orcas on only one day over almost 12 months of observation (0.08 sightings/month) at the same site. This ten-fold decrease in orca sighting frequency could indicate that orcas stopped visiting GSJ and concentrated their hunting effort in the EOC where pinnipeds are more abundant. The population of southern elephant seals increased 3.5% per year between 1982 and 2001 (Lewis and Campagna, 2002). In 2001, 98% of the elephant seal population reproduced along the Outer Coast of Valdés (Lewis and Campagna, 2002). Thus, GSJ became a comparatively less productive

hunting ground for orcas and a safer place for right whales, which moved from the EOC into GSJ and GN mostly during the 1980's (Rowntree et al., 2001).

During the 1970's, the densest concentration of right whales in GSJ occurred in Fracaso Bay (Rowntree et al., 2001), whose extensive areas of shallow water are probably optimal for avoiding orca attacks. Although right whale mothers and calves continued to use Fracaso in the 1990's, it was not a preferred area (Rowntree et al., 2001). Coincidentally, a study of gull harassment of right whales (kelp gulls feed on the skin and blubber of live right whales in this nursery ground) (Rowntree et al., 1998) showed that Fracaso has the highest frequency of gull attacks on the whales. If whales are forced to spend more time away from this shallow bay because of gull attacks, then they could be more exposed to orca attacks in other less favorable bays in GSJ.

The increase in the number of encounters observed in GN during the 1990's could be a consequence of the right whales moving into GN (Rowntree et al., 2001), the growth in their overall population (IWC, 1998; Cooke et al., 2001), and an increase in observation effort, given that whale-watching and the number of potential observers in GN grew significantly in the 1990's (Rivarola et al., 2001) compared to GSJ where human population has remained relatively small.

Implications for right whale behavioral ecology, migration and the 'predation hypothesis'

There is considerable disagreement about the frequency and intensity of orca encounters with baleen whales and how they affect baleen whale behavior. Mizroch and Rice (2006) provide a summary of reports of orca attacks on several species of baleen whales (especially minke and gray) in the N Pacific, and suggest that orcas attack healthy, adult large whales, although rarely. In Alaska, Dolphin (1987) saw 18 encounters between orcas and humpback whales in 1979-1984, none of which involved an attack, concluding that they coexist in a 'non-belligerent, if uneasy, manner'. However, the same author reported that 15-20% of 350 identified humpbacks in that area (or, at least, 52 whales) bear scars from orcas, which could only have resulted from attacks. Similarly, Clapham (2001) observed no orca attacks on humpbacks in over 20 yr in the Gulf of Maine, stating that 'there is little evidence that humpback whales are anything more than a very occasional target of killer whales anywhere'. However, Katona et al. (1980) found that 33% of approximately 2,800 humpbacks in the NW Atlantic (or, at least, 924 whales) have scars that can be attributed to orca teeth. Connor and Corkeron (2001) stress that 'a lack of observations of predation is an error that commonly leads field biologists to underestimate the importance of predation'.

Although in a smaller proportion than humpbacks in the N Atlantic, right whales in Valdés also bear scars that can be attributed to orca bites (Rowntree et al., 2001). We believe that the 976 humpbacks reported bearing orca scars in Alaska and the NW Atlantic (scars that could only have resulted from 976 attacks) as well as our reported 117 orca – right whale encounters in Valdés including 12 attacks, are evidence that orca attacks on humpback and right whales occur relatively more often than is believed at least somewhere. The fact that many attacks are not observed by humans and that we do not know where they occur, should not underestimate their frequency and potential effect on the whales' behavioral ecology. The rosette formation documented in baleen whales and in sperm whales is a behavior that must have evolved as a consequence of a relatively widespread selective pressure such as predation by orcas.

Could attacks also occur at night? If new methodologies allow us to monitor large cetaceans across their entire home ranges for longer periods, and to correlate the number of scarred whales to the number of whales actually killed by orcas, we suspect that orcas will be viewed as 'more important predators for some populations than previously believed' (Jefferson et al., 1991).

Harbour seals (*Phoca vitulina*) can discriminate calls from mammal-eating and fish-eating orcas and selectively habituate to the calls of harmless orcas (Deecke et al., 2002). If right whales were able to obtain behavioral cues from orcas acoustically, then they could also adjust their level of reaction to the orcas' proximity and behavioral state (i.e., hunting or not). This could explain the Class I and II interactions described by Dolphin (1987) and the grade 1 encounters described by us. The fact that more grade 2 encounters did not escalate to actual attacks could be evidence of successful antipredator strategies used by right whales, including increase in group size, rosette formation and combined defense.

It is generally accepted that orca density and mean school size decrease from higher to lower latitudes (Dahlheim et al., 1982; Hammond, 1984; Wade and Gerrodette, 1993; Corkeron and Connor, 1999). The mean orca group size in Valdés ranges from 2.1 (Iñíguez et al., 2005) to 3.2 (López and López, 1985), compared to 9.3 (Dalla Rosa et al., 2002) to 27 (Hammond, 1984) around Antarctica. Orcas in the S Atlantic may follow minke whales in their migrations to temperate waters (Budylenko, 1981; Mikhalev et al., 1981). However, the same individual orcas are sighted in Valdés throughout the year (López and López,

1985; Iñíguez, 2001), indicating that orcas from other areas do not follow right whales to this nursery ground. Thus, by migrating to Valdés, right whales avoid the main schools of orcas that follow minke whales to more northeastern waters of the S Atlantic in the fall and winter (Budylenko, 1981), reducing their chances of encountering large groups of orcas during half of the year when their calves are youngest.

Corkeron and Connor (1999) explain baleen whale migration by the advantages that migrating to lower latitudes confer to pregnant females to reduce orca predation on their calves. Right whale calves appear not to be the main target of orca attacks in Valdés. Here, mothers and calves swim and aggregate in shallow bays (Payne, 1986; Rowntree et al., 2001). One result of the use of such shallow water is that their three-dimensional aquatic environment becomes virtually two-dimensional, reducing the number of potential directions from which an orca attack can come. Under this view, an aggregation of right whales in these shallow bays could be compared to the 'selfish herds' of cattle described by Hamilton (1971). Assuming that right whales spend significant amounts of time in waters deeper than 5m on their summer feeding grounds (Hammer et al., 1988; Murison and Gaskin, 1988), then those grounds may be less suitable for avoiding orca attacks than the shallow waters off Valdés, promoting right whale migration to this site.

In summary, Península Valdés has features that are advantageous for right whales to reduce orca predation risk. Orca density and group size at the Península are lower compared to higher latitudes in the S Atlantic (López and López, 1985; Iñíguez, 2001; Dalla Rosa et al., 2002; Iñíguez et al., 2005), it has growing colonies of pinnipeds for orcas to prey upon (Lewis and Campagna, 2002; Crespo et al., 2003), and it has extensive areas with shallow water where right whales concentrate (Rowntree et al., 2001) probably to protect themselves from orca attacks. Hamilton (1971) stated that 'even for the most unpromising initial conditions it remains evident that predation should lead to the evolution of gregarious behavior', and that 'even in non-gregarious species selection is likely to favour individuals who stay close to others'. We believe that the 'predation hypothesis' (Corkeron and Connor, 1999) can explain at least in part the migration of this right whale population to Península Valdés. The possibility of staying close to other individuals in shallow water combined with the absence of large orca pods are important factors that could drive the annual migration of southern right whales to this nursery ground. The responses of right whales to the presence of orcas suggest that the risk of predation may be an important evolutionary force in shaping right whale social structure and behavior. Although we propose that orca predation pressure can influence habitat choice by right whales, we are still far from understanding the reasons and causes for the observed changes in right whale distribution within this nursery ground.

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