BEHAVIOR AND SOCIAL DEVELOPMENT OF JUVENILE SOUTHERN RIGHT WHALES (*Eubalaena australis*) AND INTERSPECIFIC INTERACTIONS AT PENÍNSULA VALDÉS, ARGENTINA

by

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I dedicate this work to Mora.

Para que estas jóvenes ballenas y vos crezcan juntas.

Ojalá mis sueños de ballenas llenen el mar de soplidos y coletazos para vos.

The first time I saw a whale, in 1988, I was a college freshman visiting the remote Península Valdés in Patagonia. I saw the tremendous body mass of an adult southern right whale breaching out of the water and falling on its side with a colossal splash. That day, I knew I had to study whales. What I did not know was that a long journey of personal migrations had begun, following the rhythm of the whales' lives.

After I graduated as a biologist, I sent a letter to Vicky Rowntree in Utah, who studies the whales at Valdés. A year later, we met in Buenos Aires. The following whale season I was her field assistant in Península Valdés. Each spring I left home and traveled south to Patagonia in order to study the whales for a month. After three field seasons, it became evident that I needed more training to develop my own research project. In 1998, I obtained a Fulbright Fellowship and moved to Madison to begin my doctoral dissertation with Charles Snowdon. This was the first time I moved from my family home.

The influence that Chuck and Vicky have had in my career is beyond words. Chuck taught me more than he probably suspects. Chuck has a remarkable ability (and an amazing memory) to juggle one hundred things at a time, and he does it well. He has always been available for research and for personal discussions. Every time I walked into

Chuck's office to discuss my data, I was full of questions. Every time I walked out, I had plenty of answers to continue my work. During our conversations, it was evident that I was speaking to a scientist with a great knowledge of animal behavior, but also to a person who cares about the human aspect of things. Chuck is generous in praise and very enthusiastic about his students' research. Whenever I had the chance to read a letter of recommendation written on my behalf, I thought he had made a mistake and was writing about someone else. He made me feel that the next letter in my mailbox would come from the Nobel Academy. Chuck is intellectually stimulating. His support in many aspects of my life in Madison has been essential for my well-being, and for my personal and professional growth. Thank you, Chuck!

"Vicky, I think north is there", "Mariano, I think north is *there*". Vicky and I have had this dialog (including the four cardinal points) countless times while watching whales at the Cliff Hut in Patagonia. Part of the richness of what Vicky has given to me over the years comes from the way she has opened my eyes to new horizons, helping me to see things from different perspectives. While I truly believe that I know where north is when I am standing on that cliff overlooking the ocean (although I may be wrong), I also know that without Vicky by my side, on many occasions I would have lost the direction of my professional path. I am proud to share my career with one of the world's top right whale researchers. I have always listened carefully to Vicky's opinions about science and about life, because many times her ideas have positively influenced my own. Vicky is a role model for me as a scientist as well as a person. I have been blessed with her advice and with her friendship for the past ten years, and I look forward to many more years to come. The same holds true for Jon Seger, Vicky's husband, who I think should visit the whales and us more often. Thank you, Vicky! The future looks bright!

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I probably would not be studying right whales if Roger Payne had not had the vision to start a long-term research project on right whales in Argentina in the early 1970's. As a world renowned cetologist, Roger has inspired me and many other whale researchers and whale lovers over the past three decades. His unique ideas keep us asking new questions. Roger has had a tremendous impact on behalf of the protection of all whales. Laura Payne was waiting for me at the bus stop at the Memorial Union when I scouted Madison in 1996, and thus, she was the first person I ever met here. She influenced my decission to move to this charming town, and I am glad she did. Thank you, Paynes!

Completing a Ph.D. program is not a one-person task. Help in all of its forms came to me from innumerable friends and colleagues in Madison. Every person in the University of Wisconsin, Madison plays a role in making this an outstanding academic place, and in creating an enjoyable and respectful atmosphere to live and work in. I thank each one of them. My office mates at the *Sardine Can* and at the Snowdon Lab made a huge difference in my daily life. Over the years (here goes the list), Matt Campbell, Anne Carlson, Stella de la Torre, Ramón Diaz Uriarte, Darcy Geddes, Anita Ginther, Jennifer Hilander, Christine Kwan, Cristina Lázaro-Perea, Liza Moscovice, Temitayo Oyegbile, Brian Trainor, Tina Whitney, Pablo Yepes, Sofia Zahed, and Carla Boe, Amy Hassenfus, Kate Washabaugh and Toni Ziegler, were dear friends, professional colleagues, study-buddies, spiritual counselors, plant-sitters and talking dictionaries when I needed help with my writing. All of you deserve credit!

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During my life, I have experienced very few certainties. But those few certainties have provided me with inner peace and a sense of protection wherever I go. The love and unconditional support of my mother Raquel and my brother Gastón have always been there throughout my life. Their presence is deeply rooted in myself. They have been an endless source of light at home and in my travels abroad. They are my protection in the world. From them I have learnt how to give and how to receive. They have taught me the importance of mutual respect and tolerance in all human relationships. They are mother, brother, and friends. I am the luckiest son and the luckiest brother for having them by my side. My new *hermana* Andrea came to fill an open space in my life with her sweet presence. Mora, my three-year old niece, created a new dimension in my view of the world. Her smile and her happy soul are a shining ray of joy to all of us around her. Mora was born at the same time when some of my young whale subjects were born. So, I dedicate this work to her, because I hope that this young girl and these young whales will grow up together in a better world, in a world full of whales. *Gracias, familia, por dar y por ser siempre todo lo que podría desear.*

To MV, for blending the light of Jupiter with the light of Fireflies so beautifully. The world would be a better place with more of your kind.

A AM, por abrir mis puertas, para siempre, a un mundo nuevo. Gracias por eso, donde sea que estés.

None of the above would make any sense without whales in the oceans.

ABSTRACT

The behavior and interspecific interactions of juvenile southern right whales (*Eubalaena australis*) (ages 1-4) were studied off Península Valdés, Argentina. Mother-calf separation occurred when infants were at least 11 months old. After separation, yearlings became significantly more social. Separation was relatively sudden, and maternal aggression was not observed. Social opportunities at Valdés may reduce weaning conflict.

Juveniles spent approximately half of the time alone and the remaining time socializing, primarily with other juveniles. Juveniles engaged in solitary, social and object play. Females played with calves and interacted with mother-calf pairs more often than males. Males engaged in homosexual behavior. Juvenile females displayed behavior patterns typical of adult females in mating groups. Young right whales may establish social relationships and practice behavior that is relevant during adult life at Valdés. Behavioral sex differences begin to be estalished early in the whales' lives.

A technique was developed to estimate the age of right whales based on measurements taken on lateral photographs. Multiple regression models explained three quarters of the variability in the square root of age as response variable. Rostral curvature was the best age predictor. Age prediction was most accurate for younger whales. The technique does not require disturbance of whales, and can help to improve estimates of demographic parameters based on the age of individuals.

Orcas and right whales were observed together on 117 occasions between 1971 and 2000. Behavioral responses varied from apparent indifference to high levels of activity in both species. Orca group size was highest and duration of encounters was longest during attacks. Right whale behavior patterns appeared adaptive to reduce orca predation. The relatively higher risk of predation at certain sites may influence right whale habitat choice at Valdés.

The frequency of kelp gull attacks on right whales was updated through to 2002. Attacks tripled since 1995. Mother-calf pairs were attacked five times more often than juveniles, who were attacked more frequently during interactions with mother-calf pairs. The interrelationship between whales, gulls, fishery waste and landfills is discussed, and management recommendations to decrease attack frequency are proposed.

CHAPTER 1: INTRODUCTION

JUVENILE BEHAVIOR AND INTERSPECIFIC INTERACTIONS OF SOUTHERN RIGHT WHALES (*Eubalaena australis*) AT PENÍNSULA VALDÉS, ARGENTINA

General overview and suggestions for future research

In 1970, Roger Payne and his associates at the Whale Conservation Institute / Ocean Alliance (WCI/OA), Massachussetts, began a study of the southern right whale population off the coast of Península Valdés in Argentina. Based on a technique to identify individuals (Payne *et al*. 1983, Payne and Rowntree 1984), research at Valdés has greatly advanced our knowledge of many aspects of right whale biology. We now know about right whale population dynamics and reproductive parameters (Payne 1986, Payne *et al*. 1991, Cooke *et al*. 2001), habitat use and long-range movements (Payne 1986, Best *et al*. 1993, Rowntree *et al*. 2001), accoustic communication (Clark and Clark 1980, Clark 1982, 1983), mother-infant interactions and spatial relationships (Taber and Thomas 1982, Thomas and Taber 1984) and conservation issues affecting this population (Rowntree *et al*. 1998). However, despite over three decades of continuous research, no studies to date have focused on the behavioral development and social interactions of juvenile southern right whales.

Tinbergen (1963) identified development as one of the Four Problems that are raised by the study of behavior. How do behavior patterns arise during the lifetime of an animal? What factors influence this development? Because today's juveniles are the next years' reproductive animals, one main reason to study juveniles is to comprehend how they develop adult skills that will eventually help them to increase their fitness (Janson and Van Schaik 1993). By delaying maturation, juveniles may become efficient foragers, grow to adult size and obtain the necessary experience before they can reproduce successfully.

I identified five areas of interest within this study. In Chapter 2 I provided behavioral observations of weaning in right whale yearlings and discussed the function of this period as a transition toward independent life. In Chapter 3 I described the behavior and social interactions of right whale juveniles and discussed the relevance of the juvenile stage as a preparation for adulthood. Chapter 4 presents a technique to estimate the age of juveniles whose year of birth is unknown based on head measurements taken on photographs. In Chapter 5 I summarized the information available since 1971 on right whale – orca interactions at Península Valdés, and discussed the role of orca predation as an evolutionary force that can shape the behavior and habitat choice of right whales. Lastly, in Chapter 6 I updated the frequencies of kelp gull attacks on right whales, and suggested management recommendations to reduce these interactions that affect the behavior of right whales at Península Valdés. Below, I summarize the rationale and the main findings and conclusions from these chapters. I also suggest topics for future research to help answer some of the many questions that still remain open in the study of right whale behavior and ecology.

Weaning behavior. Mother-infant separation can be a period of conflict for the two members of the pair (Trivers 1974, 1985). It is not yet clear how the behavior of right whale mothers and calves changes before they separate (Taber and Thomas 1982, Thomas and Taber 1984). To understand how behavior patterns develop in the young whales after separation, it is important to study how weaning occurs. Adult right whale females migrate over 2,000 km from the feeding grounds to Península Valdés (Best *et al.* 1993, Rowntree *et al.* 2001) to wean their yearlings there. This suggests that the Península may offer advantages for the weaning process. Separation occurred when right whale yearlings were at least 11 months old. When weaning was about to occur, yearlings consistently followed their mothers as the mothers attempted to increase the distance between the two. After separation from their mothers, yearlings became significantly more social and interacted more with whales of all age classes. The separation was relatively sudden, and we did not observe signs of aggression from the mothers toward their infants. We conclude that the right whale social environment at the Valdés nursery ground may be beneficial to reduce weaning conflict, as it offers ample opportunities for yearlings to interact with conspecifics as they learn to live independently from their mothers.

Suggestions for future research: Are the Península Valdés right whale mothers behaviorally diverse? A cautious personality negatively affects young adult male vervet monkeys trying to attain dominance in a new group, but it helps young mothers to keep their newborns alive (Fairbanks 1996). Interindividual comparisons of mother-infant and weaning behavior before and after separation may elucidate if differences in maternal style affect individual survival and reproductive success in right whales.

Juvenile behavior. The period of time between weaning and adulthood is a critical transitional stage in most mammals. Negotiating the years of juvenility before reproduction can even begin is the first great challenge of life after weaning (Pereira and Fairbanks 2002). Juvenile mammals need to become informed, to learn and to practice behavior to succeed in a fundamentally adult world (Pereira 1993, Pereira and Fairbanks 1993). Juvenile right whales are observed every year at the Península Valdés nursery ground, where they do not obtain any obvious reproductive or foraging advantage. Why do juveniles migrate to the Península? How do they spend their time there? How much time do they spend alone and in social interactions? Do they interact more with age peers, mother-calf pairs or adults? Are there sex differences in juvenile behavior? Juvenile right whales spent approximately half of the time alone and the remaining time socializing, primarily with other juveniles. Juveniles of both sexes engaged in solitary, social and object play, and in sexual behavior. Juvenile females played with calves more often than males did, and assumed an active role to maintain interactions with mother-calf pairs. Juvenile males were involved in homosexual behavior, typically with other age peers. Female juveniles displayed behavior patterns that are typical of adult females in surface active groups, such as staying belly up (possibly to avoid unwanted copulations) and turning away from males. Our findings suggest that Península Valdés may function as a place for right whale juveniles to socialize, establish relationships with other whales and to practice behavior that is relevant during adult life. Opportunities for social activities might be limited in the right whales' feeding grounds (Thomas and Taber 1984). This stresses the need to design effective conservation policies to protect this area in the long term for the normal behavioral development of right whales.

Suggestions for future research: It has been suggested that long-term social bonds in baleen whales might be more common than is currently believed (Connor 2000). Are the juvenile females that interact with mothers and calves closely related to them? Do juvenile males form alliances that are maintained during their lifetimes? Does kinship benefit juveniles to learn social behavior from adults and from age peers? Genetic analyses combined with long-term longitudinal behavioral studies can provide answers to these questions. Also, a considerable proportion of juveniles (and adults) use waters that are too distant from shore to do reliable shore-based observations of their behavior. Boat-based observations and photoidentification of the whales that use the center of the gulfs at the Península would help us to elucidate the importance of that portion of the Península's habitat for the whales.

Age estimation. Individual right whales can be identified by the unique pattern of callosities on their head (Payne *et al*. 1983, Kraus *et al*. 1986). When calves are born, the head is small and the callosity pattern is often covered by dense patches of cyamids or "whale lice" (Rowntree 1996) that hinder individual identification from aerial photographs. Consequently, many right whales cannot be identified in their year of birth and thus their age is unknown. Important demographic parameters are based on the age of individuals. Thus, we developed a technique to predict age in right whales based on a combination of allometric measurements taken on lateral shipboard photographs of North Atlantic right whales. The North Atlantic Right Whale Consortium database was chosen to do this study because it has an extensive photographic record of individuals identified from boats. These shipboard photographs provide the necessary lateral perspective of the head of right whales to take the measurements. We used multiple regression to build prediction models for different photographic qualities. The models explained three quarters or more of the variability in the square root of age as response variable. Rostral curvature and dome height showed the greatest variation with age and thus, were the best anatomical predictors of age. Model fit was lower for whales with continuous callosity patterns. Age prediction was most accurate for younger whales. The technique is easy to apply, has low cost and does not require to kill or even disturb the whales. It can be a valuable tool to improve estimates of population parameters that are based on the age of the individuals.

Suggestions for future research: Because right whale surveys in the southern hemisphere are primarily aerial based, the compatibility of shipboard and aerial photographs for the application of this technique should be explored to design a smilar age prediction model for right whales based on aerial photographs. Other techniques (Whitehead and Payne 1981, Best and Rüther 1992) should be combined to increase prediction accuracy.

Orca predation. Because of the fatal outcome of a failed escape from an attack, predation pressure has been recognized as a strong selective force that can shape the behavior of prey species (Lima and Dill 1990). Orcas are top predators of marine mammals. Orcas and right whales coexist in the waters surrounding Península Valdés for about six months each year. Corkeron and Connor (1999) have proposed that reduced predation risk on baleen whales from the abundant orcas found in high latitudes provides the primary fitness benefit to baleen whales migrating from polar waters to lower latitudes to give birth (the "predation hypothesis" for baleen whale migration). We propose that right whales exhibit behavior patterns that have evolved to reduce predation risk, and that the relatively higher risk of orca predation at certain sites can influence habitat choice by right whales at Península Valdés. We report on 117 encounters between orcas and right whales (including 12 attacks) that were observed between 1971 and 2000. Behavioral responses varied from apparent indifference to high levels of activity in both species. During the attacks, orca group size was highest and the duration of the encounters was longest. Most encounters occurred along the Eastern Outer Coast of the Península, an area that has been abandoned by right whales since the 1970's (Rowntree *et al*. 2001). Right whales displayed behavior patterns (such as use of the tail as a weapon, use of shallow waters, "rosette" formation) that could be adaptive to reduce predation. Although at present we cannot conclude that orca predation has caused the observed changes in habitat use by right whales, our data suggest that predation can influence right whale habitat use and appear to support the predation hypothesis for the migration of southern right whales to this nursery ground.

Suggestions for future research: Corkeron and Connor (1999) identified inter-population comparisons of orca predation rates on right whales as one way to assess the predation hypothesis. Natural "field tests" of the predation hypothesis will be possible when comparable data to those presented here become available for orca and right whale populations at other sites.

Gull harassment. Kelp gulls at Península Valdés have developed the habit of feeding on skin and blubber that they gouge from the backs of southern right whales

(Thomas 1988, Rowntree *et al*. 1998). This has a negative impact on the whales, who respond to the attacks of gulls by flinching violently and swimming away. This response increases energy expenditure, interrupts nursing bouts, social interactions and resting. The local kelp gull population has expanded in the last two decades possibly as a consequence of the food provided by the fishery industry at landfills (Bertellotti *et al*. 2001, Giaccardi and Yorio in press). The parasitic behavior of gulls has spread in the population, and the frequency of the attacks has increased over time (Rowntree *et al*. 1998). We updated the frequency of gull attacks through to 2002. The frequency almost tripled between 1995 and 2002. Gulls directed most attacks to right whale mother-calf pairs, who were attacked five times more often than juveniles. The attack rate per hour on juvenile whales was highest during interactions with mother-calf pairs and lowest during interactions with adults. We discuss the interrelationship between whales, gulls, fishery waste and landfills, and propose management recommendations to decrease the frequency of the interactions. The recommendations include to improve waste management practices (covering the fish refuse, recycling), explore gull dispersion methods at landfills, and monitor the frequency of gull attacks to evaluate the effectiveness of any action taken to reduce the problem.

Suggestions for future research: To design an effective conservation strategy it is critical to determine the proportion of gulls that feed on the whales. Although our results support the hypothesis that relatively few gulls specialize in feeding on whales, this remains to be tested with field experiments involving marking individual gulls. Lobbying at the local government level is essential to work cooperatively toward the solution of this conservation problem.

The relevance of a study on juvenile behavior and its implications for right whale conservation

It has been recognized that despite obvious areas of common interest, there has been little mixing of behavioral and conservation biology (Sutherland and Gosling 2000). Behavioral studies can combine theoretical approaches with practical applications that can be useful in wildlife management and environmental preservation (Martin and Bateson 1993, Blumstein and ABS 2002).

Right whales were hunted for centuries and are now the most endangered of all baleen whales. Hunting in the southern hemisphere reduced the right whale population from an estimated 55,000-70,000 animals before commercial whaling to 7,500 at present (IWC 2001). Although some populations are recovering (*e.g.*, South Africa, Best *et al*. 2001, Argentina, Cooke *et al*. 2001), all cetaceans in all oceans now confront the most serious long-term threat: habitat degradation (Whitehead *et al*. 2000, Burns 2001). This is especially true for coastal cetaceans like the right whale. Right whale researchers have the responsibility to learn as much as possible about right whale biology, behavior and ecology, and to apply that knowledge to protect them in the long term.

Research to understand the juvenile period can help characterize the role of experience in regulating the development of animal life histories (Pereira 1993). Robust, longitudinal data on juvenile behavior can be used to learn about sex differences in life histories and can improve comparative studies on the evolution of behavior (Pereira and Fairbanks 2002). Juveniles are smaller, weaker, less experienced and are challenged by the environment in different ways than adults (Pereira and Fairbanks 2002). Thus, if we are to have an integral knowledge of the life histories of right whales to protect them, it is important to know about the behavior of juveniles and their social and ecological needs. The long life-spans, slow reproductive cycle and vulnerability of right whales, strengthen the need to carry out such studies.

Juvenile whales are particularly vulnerable as they learn to live independently from their mothers. Juvenile whales have relatively high mortality compared to other age classes (Sumich and Harvey 1986, Dunbar 1987, Kraus 2002). Research that focuses only on adult animals is inherently biased toward those successful individuals that survived the juvenile stage (Pereira and Fairbanks 2002). Therefore, understanding the needs of all age classes can help to determine the conservation requirements of a species. Southern right whales are presently protected from the whaling industry, but there is plenty of economic incentive to resume commercial hunts (Whitehead *et al*. 2000). Studies of the behavioral diversity of juveniles and adults are necessary to evaluate the effects of potential commercial exploitation in the future (Reynolds and Jennings 2000).

The Península Valdés nursery ground may be just as important to juvenile right whales as to mothers and calves: they have similar resighting patterns and use similar areas in the nursery ground (Rowntree *et al*. 2001). Juvenile right whales have a high between-year resighting frequency at Península Valdés (Rowntree *et al.* 2001). However, we know little about how juvenile right whales spend their time there and about the benefits they gain from migrating over 2,000 km to spend several weeks in this nursery ground each year.

If sufficent data can be gathered, studies of cetaceans based on repeated focal follows of known individuals can determine patterns of behavior, movement and association in juveniles and adults of both sexes (Clapham 2000). Despite their high resighting frequency, the chances of observing known juveniles for longitudinal behavioral studies at the same location can be reduced at Península Valdés by the relatively large size of the population (2,577 whales in 1997, IWC 1998) and by the extensive coastline of the Península (495 km) along which the whales distribute (Rowntree *et al*. 2001). For instance, in the present study, juveniles that were identified in their year of birth in Golfo San José were seen as yearlings at a site 260 km away in Golfo Nuevo and *vice versa*. To have several observers searching for known individuals along the coastline in the areas where the whales concentrate would increase resighting rates and improve results and conclusions.

Also, because juvenility is a transitional period, known juveniles can be followed for a restricted period of time before they become adults. This naturally reduces the number of known subjects that are available for any longitudinal study. Behavioral studies based *solely* on resightings of known individuals in such large populations and areas should be evaluated carefully. Longitudinal and cross-sectional studies should be combined. Caution should be excercised when reporting and analyzing behavioral data generated from observations of known (resighted) and unknown individuals. The differential contribution of repeated resightings of few individuals *vs*. isolated follows of non-resighted whales to the datasets should be properly accounted for.

Assessing the impacts of human activities on animal behavior is necessary to know the consequences of human disturbance on the population (Gill and Sutherland 2000). Juvenile North Atlantic right whales are particularly vulnerable to entanglements in fishing gear and to ship collisions, the main causes of anthropogenic mortality in right whales (Kraus 2002). Ship traffic is increasing at Valdés and there are projects to develop a seed mussel industry there. Whale watching has also evoked concern with regard to right whale behavior (Katona and Kraus 1999). The expanding ecotourism industry in Patagonia, largely based on right whales, can directly affect their behavior (Garciarena 1988, Rivarola *et al.* 2001). It can also impact the whales in indirect ways. For instance, in 2002 a juvenile right whale became entangled in the mooring chains of a whale-watch boat at Península Valdés. Presently, in many circumstances, wildlife mananagement decissions are made with limited data (Blumstein and ABS 2002). The information obtained from a study on right whale juvenile behavior can contribute relevant information to estimate the potential impact that these commercial activities can have on the health and survival of the overall population.

An effective way of linking science to conservation is by educating local people who are in close contact with the wildlife. The whales generate a strong attraction in thousands of people who travel from all over the world to remote areas like Patagonia to see them (Payne 1995). Local inhabitants can become educators of increasing numbers of visitors, who in turn go back to their homes and share with family and friends what they learned about the whales. Scientific findings about the behavior of whales should be used for educational purposes in popular articles. Whales are a powerful symbol for environmental conservation, and public support for the whales in Argentina is growing. Educated people can become actively involved and can pressure governments to sustain conservation initiatives to protect the whales and their marine environment.

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CHAPTER 2

WEANING TIME AND BEHAVIOR OF SOUTHERN RIGHT WHALES (*Eubalaena australis*) ON A NURSERY GROUND AT PENÍNSULA VALDÉS, ARGENTINA

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ABSTRACT

The care of the young by adult baleen whale females ends with weaning. It is important to study how weaning occurs in order to understand how behavior patterns arise in the young whales after separation from their mothers. We observed and quantified the behavior of yearling southern right whales (*Eubalaena australis*) before and after separation from their mothers during the peak of the calving season (Aug to Nov) at the Península Valdés nursery ground in Argentina. Yearlings were weaned at a mean minimum age of 11.2 mo between mid-Aug and mid-Sep. There were no significant differences in the time yearlings spent traveling, surface active or underwater before and after separation. However, after separation, yearlings spent significantly more time resting and socializing with whales of all age classes. Social time increased from 7.2 % before separation to 22.2 % during the first two to nine weeks after separation. When weaning was about to occur, mothers consistently increased their distance to the yearlings, who were primarily responsible for maintaining proximity (mean Proximity Index = 86.3 for seven pairs). The presence of other right whales in a relatively small area at this nursery ground may be beneficial for the social development of yearlings as they learn to live independently from their mothers. Opposing interests in the needs of yearlings to nurse and their mothers' needs to replenish energy reserves for their next pregnancy may cause weaning conflict in southern right whales. However, weaning appears to occur in a short period of time and without apparent aggression from the mothers toward their young.

INTRODUCTION

Conflict between parent and offspring over the length and over the amount of parental investment provided has been widely observed in mammals such as carnivores, ungulates and primates (Trivers 1974, 1985). This conflict is expected to increase throughout the period of parental care and especially during the time of weaning (Trivers 1974).

Baleen whales are generally seasonal breeders whose reproductive cycle is linked with migration to ensure optimum conditions for survival of the single calf (Lockyer 1984). In most baleen species, weaning may occur around the end of the calf's natal year (Lockyer 1984). For instance, most humpback whale (*Megaptera novaeangliae*) mothers and calves remain associated for one year, although the duration of this association is variable (Baraff and Weinrich 1993, Clapham 1992, 2000). Recorded weaning times in North Atlantic right whales (*Eubalaena glacialis*) show considerable variability, spanning from 8 to 17 months and being most common within the first 12 months of the calves' life (Hamilton *et al.* 1995).

In southern right whales (*Eubalaena australis*), permanent separation from the mother occurs when calves are 12 to 15 months old (Taber and Thomas 1982, Burnell 2001). Female right whales typically calve once every three years, and stay in nursery grounds such as Península Valdés with their calves for the first two to three months post-partum (Payne 1986, Best and Rüther 1992, Cooke *et al.* 2001). During this time, calves grow 2-3 m in length (Whitehead and Payne 1981, Best and Rüther 1992) and develop locomotory and social skills (Taber and Thomas 1982, Thomas and Taber 1984). Cow-calf pairs then migrate to their feeding grounds (Best *et al.* 1993), and some return when the calves are almost one year old (Thomas and Taber 1984, Rowntree *et al*. 2001). Mature females in their calving years show significantly higher fidelity to the nursery grounds than males, and they return repeatedly to calve and to wean calves at particular locations (Burnell 2001, Rowntree *et al.* 2001). The fact that adult females that will neither forage nor mate migrate to Valdés with their one-year-old calves probably to wean them there (Thomas and Taber 1984, Rowntree *et al.* 2001), suggests that there must be important advantages for yearlings to be weaned in this area.

Newborn right whales in Valdés stay in close proximity to their mothers (Taber and Thomas 1982). It is not clear how the behavior of mothers and yearlings and their spatial relationships change before the final separation takes place (Thomas and Taber 1984). The International Whaling Commission dictates that female whales accompanied by calves cannot be taken (IWC 1977). Hence, although right whales are not hunted at present, it is important for management purposes to determine when a calf has permanently separated from its mother (Clapham *et al*. 1999). Due to short sampling time (less than 7 h) and to the small number of individual yearlings observed (three), Thomas and Taber (1984) suggested replication of their observations would be necessary to describe weaning in right whales. Here we present behavioral observations of southern right whale mother-yearling pairs at Península Valdés before and after separation. We estimate the age of yearlings at weaning and the timing of separation during the nursing season. We provide evidence of changes in the role to maintain proximity in the two members of the pair, and of increased socialization of yearlings after separation from their mothers.

MATERIALS AND METHODS

Data were collected during the 1999 to 2001 southern right whale calving seasons (Aug to Nov) from an Observation Hut (42º25'S, 64º9'W) built on a cliff-top at 45 m above sea level at Península Valdés, Argentina. We identified individual whales by their distinctive callosity patterns and body marks (Payne *et al.* 1983, Payne and Rowntree 1984). In this paper, the term "calf" refers to whales seen at Valdés during their season of birth in close association with their mothers. The term "yearling" refers to whales seen at Valdés during their second season with or without their mothers. Mother-calf (MC) pairs were identified in the calves' year of birth and resighted in the following season before and after separation of the mother-yearling (MY) pair. Yearlings were considered to be weaned when they were seen without their mothers and their mothers were not seen at the study site on the same day for at least two consecutive sightings on two separate days. Visual scans of the study site were done every hour to search for known individuals.

We used a 20X wide-angle spotting scope mounted on a tripod to visually follow the whales for distances of up to 2 km. We recorded the behavior of yearlings by continuous focal animal sampling (Altmann 1974) using a Hewlett Packard 48GX programmable calculator that automatically logged the duration (in sec) of each behavior pattern. The behavior of the mother in a pair was noted on paper. We did not collect behavioral data on MC pairs. Instead, for our comparisons we used Taber and Thomas (1982) and Thomas and Taber (1984) behavioral descriptions of 21 MC pairs based on 115 h of observation at the same site. We noted the dates when MC pairs were observed to estimate the minimum age at separation in yearlings by counting the number of days between their first sighting as calves and their first sighting as yearlings without their mothers.

Four behavioral categories were considered. A whale was "resting" when it was motionless and horizontal at the water surface (or slightly beneath it, only surfacing to breathe). A whale was "traveling" when it swam to change location, leaving "footprints" or surface swirls in the trailing path caused by the motion of the tail flukes. A whale was "surface active" when it caused white water with the movements of its body (including rolling, flipper and tail slapping, breaching, and locomotory patterns involving another whale). A whale was "underwater" when it was submerged and its behavior could not be recorded for 30 sec or longer.

We recorded the sociability of yearlings. A yearling was "social" when there was at least one other whale besides its mother within a five whale-length (WL) radius from it. Otherwise, the yearling (or the MY pair) was “solitary.” The 5 WL limit was chosen because it was assumed that whales that were 5 WL appart or more were not in visual contact, although accoustic contact was likely. Interactions between the two members of a MY pair were “asymmetric” when one member (the “actor”) had an active role in maintaining the interaction with the other member (the “recipient”) (*e.g.*, by approaching the other member to decrease the distance between the two, by circling around it or by seeking physical contact). Otherwise, the interaction was “symmetric” (*e.g.*, the two whales were resting or traveling side by side in the same direction at less than 5 WL from each other).

We counted the number of times each member in the MY pairs approached (actively moved toward) and left (actively moved away from) the other member (Taber and Thomas 1982). We calculated the difference between the percentage of approaches and leaves due to the yearlings and due to the mothers, and obtained a Proximity Index for each pair (Hinde and Spencer-Booth 1967, Hinde and Atkinson 1970, Thomas 1986). Positive results would indicate that the yearling was primarily responsible for maintaining proximity (a value of 100 indicating that the yearling was totally responsible), and negative results would indicate that the mother was (a value of -100 indicating that the mother was totally responsible).

A total of nine yearlings were observed. Four yearlings (Furadito, Tricola, Tridentito and YD140801) were followed only before separation, two (Hueso and Puntas) were followed only after separation, and three (Mochita, Lluvia and Rombita) were followed both before and after separation. For behavioral comparisons before and after separation, we placed each of the latter three individuals in the condition for which they were observed for the longest time to avoid non-independence between samples. Mochita and Lluvia were with their mothers for 86 % and 74 % of their total observation time, respectively. Follows of these two yearlings were added to the pre-separation sample (totalling six MY pairs before separation). Rombita was observed without her mother for 83 % of the time. Follows of this yearling were added to the post-separation sample (totalling three yearlings after separation). For tests that did not involve comparisons between the two conditions, follows of these three yearlings were used both in the pre-separation sample (totalling seven MY pairs) and in the post-separation sample (totalling five yearlings). Three yearlings (Hueso, Mochita and Rombita) were females and two (Puntas and Lluvia) were males. We could not determine the sex of the remaining four yearlings.

Time proportions for behavioral categories and sociability of yearlings before and after separation were calculated. Proportions were normalized by the arc sin of the square root for statistical analyses and comparisons. However, in the results we provide means ± standard deviations of real time percentages for descriptive purposes. Focal follows of known yearlings within the same season were pooled and treated as one sample for that season for each resighted subject to avoid pseudoreplication (Mann 1999). Comparisons of the time yearlings spent under the four behavioral categories before and after separation, and in solitary and social conditions, were done with the Student t-test. The Sign Test was used to test the significance of the results obtained for the Proximity Index for seven mother-yearling pairs. Statistical tests were carried out using SPSS version 11.0.1 for Windows (SPSS Inc. 2001). Tests were two-tailed and the level of significance was set at $\alpha = 0.05$.

RESULTS

We recorded the behavior of nine yearlings in 47 focal animal samples for a total of 53.7 h of continuous observation (Table 1). We collected between 1 and 11 focal samples per subject (x = 5.2). After pooling follows of resighted individuals, the average duration of focal observation per subject was 5.97 ± 5.66 h (range = 0.45 – 16.10 h). Of the total observation time, 22.9 h and 30.8 h were obtained before and after separation, respectively (Table 1).

The mean minimum age at weaning of the five yearlings that were observed after separation was 11.2 mo or 337 ± 8.58 d (range = 328 – 350 d) (Table 2). The mean minimum age of three yearlings when last seen with their mothers was 11.1 mo or 332 ± 6.43 d (range = 325 – 337 d). Four whales were first identified as calves in mid- to late September and one in October, and were first seen without their mothers between mid-August and mid-September of the following year (Table 2). Most births in Valdés occur in August (Whitehead and Payne 1981). Using August 15 as the possible birth date of the five yearlings observed after separation, their mean age at separation was 12.6 mo or 377 ± 15.57 d (range = 364 – 395 d).

Before separation, the seven MY pairs spent 76.3 ± 13.9% of the time in symmetric interactions (mostly traveling side by side, with the mother leading the direction of travel, or resting) and the remaining 23.7 ± 13.9% in asymetric interactions, when one member of the pair had an active role in maintaining contact. During asymmetric interactions, yearlings spent significantly more time as actors than as recipients (paired t = 14.18; df = 6; $P < 0.001$). The mothers were the focus of the yearlings' activities. Yearlings spent virtually all the time (96.6 ± 4.3%) during asymmetric interactions approaching their mothers, stroking them with their flippers, circling around them and rolling on the mothers' backs, while the mothers repeatedly turned away and rarely initiated physical contact with their yearlings. The Proximity Index was positive for the seven MY pairs observed before separation (x = 86.3 ± 17.1; range = 66.7 – 100; Sign Test, N = 7, P = 0.016) (Table 3). When only the two MY pairs (Lluvia and Mochita) for which over 30 approaches and leaves were observed are used, the mean Proximity Index decreased (68.7 ± 2.1) but was still high. This indicates that yearlings were primarily responsible for maintaining proximity in the pairs.

The number of days between the first and last sightings of yearlings after separation ranged from 15 to 65 d (Table 2). Fig. 1 shows the overall behavior of yearlings before (N = 6) and after (N = 3) separation. While travel time decreased after separation, there were no significant differences in the time yearlings spent traveling, surface active and underwater between the two conditions. However, resting time significantly increased after weaning (independent samples t-test = 4.58; df = 7; P = 0.003) (Fig. 1). Mother-yearling pairs spent most of their time (92.8 ± 3.8%) alone (Fig. 2). In contrast, after separation, yearlings spent significantly less time alone (77.8 ± 11.2%; independent samples t-test = 2.71; df = 7; P = 0.03) and more time socializing (22.2 ± 11.2%; independent samples t-test = 4.2; df = 7; P = 0.004) with whales of all age classes than before separation.

Observations of yearling Mochita and her mother provide some insight on how the final separation takes place. On the second to last day that female yearling Mochita was observed before separation (August 19, 2000), her mother fed for 55 min. Mochita briefly followed the mother and then turned away until the maximum distance between them was over 1 km. Mochita then approached her mother and stayed in close proximity for over 4 h, repeatedly stroking the mother with her flippers and flukes. Mochita attempted to nurse at least four times while her mother swam away, and Mochita followed her at 1 WL or less. On September 9 the pair was seen together for the last time. Mochita swam around her mother at less than 1 WL for about 5 min while the mother stayed belly up, possibly to prevent her young from nursing. Mochita then interacted with the calf of a nearby MC pair for 10 min. At this time, her mother turned away and traveled east for 20 min before we lost sight of her, while Mochita traveled west and separated from her mother for a distance of at least 2 km before we stopped following her. On September 12 we observed Mochita interact with two other juveniles of similar size for 80 min. Her mother was not sighted at the study site after September 9, while Mochita was seen on three separate days until September 27. We did not observe any apparent aggression from the mother to the yearling in this or in any other MY pair throughout this study.

DISCUSSION

The minimum age at separation reported here supports the suggestion that right whales, like other baleen whales (*e.g.*, humpback whales, Clapham 1992; bowhead whales, Koski *et al.* 1993) are most commonly weaned at around one year (Hamilton *et al.* 1995, Taber and Thomas 1982). It seems likely that most southern right whale yearlings are weaned in August and September (Thomas and Taber 1984). We do not know the proportion of right whales that are effectively weaned at Valdés. It appears to be high, given the relatively high resighting frequency of yearlings (0.51) compared to other age classes at the Península (second only to adult females in years when they calved = 0.53, Rowntree *et al.* 2001). This implies that this nursery ground may offer important advantages for right whales to be weaned there.

Right whales may have few opportunities for socialization at their feeding grounds (Thomas and Taber 1984). Female baleen whales with their calves are more solitary than other individuals (Clapham 1994, Hamilton 2002). The sociability of right whale yearlings increased immediately following separation from their mothers at Valdés. This suggests that the proximity of other right whales for potential interactions may be beneficial for the initial social development of the young whales as they learn to live independently from their mothers. Additionally, the concentrations of right whales in the shallow bays of Valdés may provide group protection against orca predation to the whales that are weaned there (Sironi *et al. in prep.*). Gray whale yearlings are particularly vulnerable to orca predation after weaning (Sumich and Harvey 1986, Ternullo and Black 2002).

Before separation, most travel time for yearlings was spent following their mothers. As a consequence of separation, the following behavior of yearlings (Thomas and Taber 1984) necessarily decreased (and their total travel time also decreased) while resting time significantly increased. No changes in the proportion of time spent in surface activities were observed. However, before separation, the mothers were the center of those activities (Taber and Thomas 1982). After weaning, surface activities involved whales other than the mothers, or solo locomotory behavior patterns such as play (Sironi and Snowdon *in prep*.).

Parent-offspring conflict might be evidenced by the shift in the role of each member of the pair in maintaining physical proximity when weaning is imminent (Trivers 1974, 1985). For instance, after birth rhesus monkeys leave their mothers more often than they approach them, but with time the responsibility for maintaining proximity shifts to the infants until the final separation occurs (Hinde and Spencer-Booth 1967, Hinde and Atkinson 1970). Similarly, right whale newborn infants often leave their mothers, who consistently approach their newborn calves (Taber and Thomas 1982). We observed the opposite pattern before weaning, as yearlings frequently turned toward their mothers when their mothers swam away. Our results based on seven mother-yearling pairs are consistent with the observations of Taber and Thomas (1982) based on three pairs, although the average value of our Proximity Index was over three times greater than that reported by Taber and Thomas. This difference could be due to different timing of the observations. We observed MY pairs in August and September, whereas Taber and Thomas (1982) observed them from June to August. It is possible that the mothers' tendency to leave their yearlings was less apparent earlier in the season.

The observations of Mochita and her mother revealed behavioral and spatial changes in the pair when separation was about to occur. Mochita's attempts to nurse were repeatedly curtailed by her mother (who swam away or stayed belly-up at the surface) (Payne 1995), and the two members of the pair separated to the longest distances recorded on any observation during this study. On one day the mother fed while Mochita followed her with her mouth closed. Little food is available for right whales at Valdés

(Payne 1986) where mothers rely on their fat reserves for nursing their young (Rowntree *et al.* 1998). Lactating females may suffer depletion of their energy resources and are unable to replenish them on a daily basis, thus showing a greater conflict with their yearlings as the season progresses (Trivers 1974). However, we did not observe overt aggressive displays from the mothers to their yearlings, such as tail slashing or use of callosities as a weapon (see Payne and Dorsey 1983). Instead, the mothers simply swam away from the yearlings as separation approached. Maternal aggression in bottlenose dolphins may occasionally play a role to reduce the close association between mothers and their calves (Connor *et al*. 2000). The frequent stroking and petting directed by right whale yearlings toward their mothers is likely to have a social function that could be compared to grooming in primates (Lazaro-Perea *et al*. in press, and references therein). Newborn bottlenose dolphins also rub and pet their mothers as a form of affiliative contact (Mann and Smuts 1999).

Separation between mothers and yearlings occurred early and rapidly compared to recorded weaning times in odontocetes (up to six years in bottlenose dolphins, Connor *et al*. 2000). It has been suggested that sudden and early weaning may be an appropriate strategy for baleen species, whose planktonic food is relatively easy to catch and does not require learning sophisticated hunting techniques (Whitehead and Mann 2000). Many aspects of social behavior are density dependent and may be affected by low population density (Anthony and Blumstein 2000). We propose that the right whale social environment at Península Valdés provides an important added benefit for yearlings to be weaned there *vs*. at the feeding grounds, where whales may be more dispersed and opportunities for social interactions may be limited. Newborn bottlenose dolphins may gain social experience and develop bonds when they separate from their mothers and interact with peers (Mann and Smuts 1998). The proximity of right whale conspecifics during weaning possibly helps to reduce the need for aggression on the mothers' part, as the yearlings increase their socialization with other whales. Thus, nursery grounds such as Península Valdés may be vital not only for the newly born calves but also for yearling southern right whales during their transition into independent life.

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FIGURES

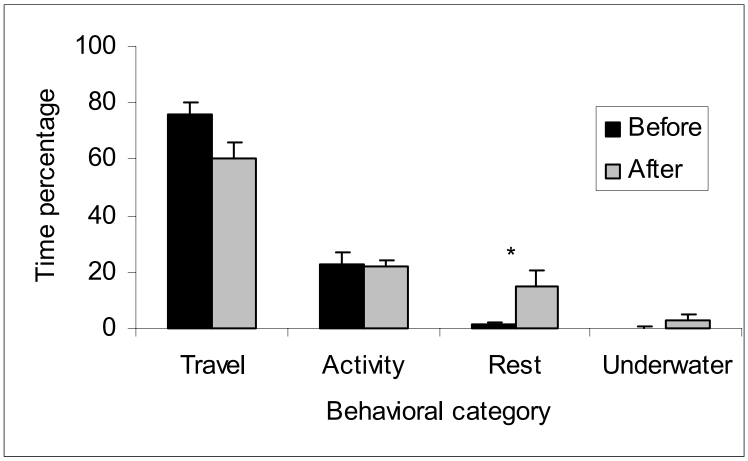

Figure 1. Mean (± SE) percentage of time yearlings spent under four behavioral categories before (N = 6) and after (N = 3) separation from their mothers. Resting time in yearlings increased significantly after separation (t = 4.58; df = 7; P = 0.003).

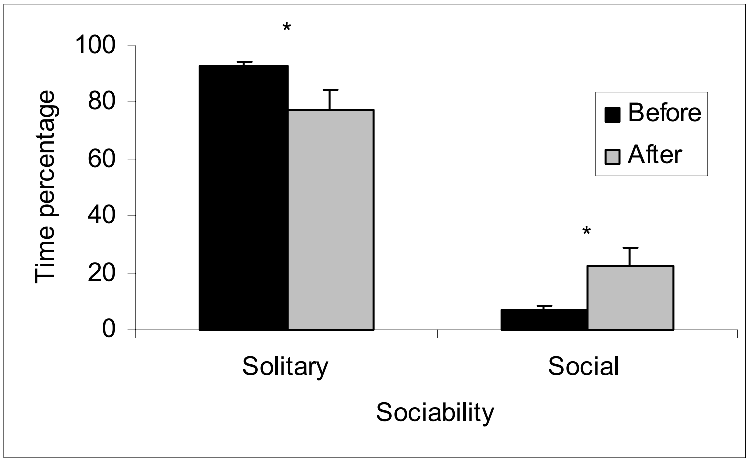

Figure 2. Mean (± SE) percentage of time yearlings spent alone or socializing before (N = 6) and after (N = 3) separation from their mothers. Solitary time significantly decreased (77.8 %; t = 2.71; df = 7; P = 0.03) and social time significantly increased (22.2 %; t = 4.2; df = 7; P = 0.004) after separation.

TABLES

Individual	Sex	Before	After	Total
Hueso	F		488 (8)	488 (8)
Mochita	F	668 (6)	113 (2)	781 (8)
Rombita	F	168 (1)	798 (10)	966 (11)
Lluvia	M	293 (4)	108 (2)	401 (6)
Puntas	M		343 (8)	343 (8)
Furadito	?	27 (1)		27 (1)
Tricola	?	89 (2)		89 (2)
Tridentito	?	93 (2)		93 (2)
MYD140801	?	35 (1)		35 (1)
TOTAL		1373 (17)	1850 (30)	3223 (47)

Table 1. Observation time in min (and number of follows) for nine yearlings before and after separation from their mothers.

Individual	First MC	Last MC	First MY	Last MY	First Y	Last Y	Age MY	Age Y
Mochita	10/19/99	10/19/99	8/14/00	9/9/00	9/12/00	9/27/00	325	328
Puntas	9/20/99	9/20/99			8/17/00	10/20/00		331
Rombita	9/11/99	9/14/99	8/12/00	8/12/00	8/14/00	10/19/00	335	337
Hueso	9/10/99	11/12/99			8/16/00	10/15/00		340
Lluvia	9/29/00	10/15/00	8/19/01	9/2/01	9/15/01	10/18/01	337	350
Mean*							332(6.4)	337(8.6)

Table 2. First and last dates (mo/d/yr) mother-calf pairs (MC), mother-yearling pairs (MY) and yearlings alone (Y) were observed for the five yearlings that were observed after separation. The last two columns are the minimum age (in days) of yearlings when they were last seen with their mothers (Age MY) and first seen without their mothers (Age Y). *Mean (and standard deviation) rounded to the nearest day.

	Yearlings		Mothers			
Individual	A	L	A	L	A + L	Index
Tricola	4	1		2	7	66.7
Lluvia	22	5	3	19	49	67.2
Mochita	20	4	1	12	37	70.2
Furadito	3			2	5	100
MYD140801	4			3	7	100
Rombita	5			4	9	100
Tridentito	6			6	12	100
Total	64	10	4	48	126	

Table 3. Number of approaches (A) and leaves (L) due to yearlings and their mothers for the seven pairs that were observed before separation, and their corresponding Proximity Index. Average Proximity Index = 86.3.

CHAPTER 3

BEHAVIOR AND SOCIAL INTERACTIONS OF JUVENILE SOUTHERN RIGHT WHALES (*Eubalaena australis*) AT PENÍNSULA VALDÉS, ARGENTINA

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ABSTRACT

Juvenile whales represent a large proportion of all whales but we know little about their behavior and social interactions and how they develop social skills to become successful adults. We studied the behavior of southern right whale (*Eubalaena australis*) juveniles (1 to 4 yr) during the calving season (Aug to Nov) between 1997 and 2001 at Península Valdés. In 1,115 hourly scans, 1,651 juveniles represented 16 % of 10,331 whales counted (including resightings). The number of whales of each age class varied throughout the season. We counted two juveniles per scan on average from mid-Aug until late Sep and then the number decreased to less than one in late Nov. A total of 29 juvenile females, 42 males, and 120 juveniles whose sex could not be determined were observed during 283.4 h of continuous focal animal samples. Juveniles engaged in solitary, social and object play. Social play with mothers and calves was more common in females than in males. Over half of the groups in which female juveniles engaged in

sexual behavior contained adult males. Over half of the groups where juvenile males engaged in sexual behavior contained only male whales. Six juveniles fed between mid-August and late October, and at least one did on *Euphausia* spp. and calanoid copepods. Juveniles spent nearly half of the time socializing with conspecifics. Solitary juveniles spent significantly more time traveling and resting and less time in surface activities than social juveniles. Juveniles of both sexes spent most of their socializing time with age peers, followed by mother-calf pairs and adults. Juvenile females spent significantly less time with other juveniles and more time with adults than juvenile males. Juvenile males initiated four times more interactions with other juveniles and fewer interactions with mother-calf pairs than expected from the age class distribution. Juvenile females and males actively maintained interactions with mother-calf pairs and with age peers, respectively. During social interactions, females spent significantly more time belly up than males (probably to avoid unwanted copulations), and ended encounters more frequently by turning away from other whales. Juvenile right whales may use the Península Valdés nursery ground as a place to practice locomotory behavior and to socialize with conspecifics. Juvenile males may establish relationships with age peers that could be important during their adult lives. Juvenile females actively seek to interact with mothers and calves, possibly to learn maternal behavior by observing them. Sex differences in social interactions that are part of adult whale behavior begin to be established during the juvenile stage in southern right whales.

INTRODUCTION

Juvenility begins when a young individual can survive the death of its mother and ends when sexual maturity is reached (Janson and van Schaik 1993). Environmental feedback, including social learning and practice, is thought to play an important role in juvenile development (Pereira 1993). Juveniles are energetic, uninformed and therefore curious animals whose main task is to become informed to succeed in a fundamentally adult world that challenges them in distinct ways and exposes them to ecological risk (Janson and van Schaik 1993, Pereira and Fairbanks 1993, 2002). Although this transitional period represents a significant proportion of the lifespan of many mammals, little is known about juvenile mammals in general.

Juveniles and adults have different energy requirements: typically, growth and development for juveniles *vs.* reproduction for adults (Clapham 2001). Research that focuses only on adult animals is inherently biased toward those successful individuals that survived the juvenile stage (Pereira and Fairbanks 2002). Juvenile whales have high mortality relatively to adults (Sumich and Harvey 1986, Dunbar 1987, Kraus 2002), as they learn to live independently from their mothers. Because juvenile and adult life history traits are closely related (Charnov 1991), it is important that we study the biology of juveniles as well as adults to understand the natural history and conservation requirements of any species.

The southern right whale (*Eubalaena australis*) population off Península Valdés in Argentina has been studied since 1970 (Payne 1986). Southern right whales migrate over 2,000 km from their feeding grounds to this nursery ground, where little food is available to them (Payne 1986, Best *et al.* 1993). Adults engage in mating behavior and pregnant females give birth to their calves (Payne 1986, Payne *et al.* 1991). It has been suggested that juvenile female baleen whales should stay in productive waters to increase their mass (Whitehead and Mann 2000). However, juvenile right whales migrate to Valdés, where they do not obtain any obvious foraging advantage, suggesting that they must be gaining something else during their time in the area. The waters surrounding the Península may be just as important to juvenile whales as to females with young calves (Rowntree *et al.* 2001). Both age categories show similar resighting patterns and use similar areas (Rowntree *et al.* 2001). Yet, little is known about the behavior and social interactions of juvenile southern right whales in this nursery ground.

When calves are approximately one year old and they separate from their mothers (Hamilton *et al.* 1995, Sironi and Snowdon *in prep.*), socialization increases (Thomas and Taber 1984). Juvenile humpback whales increasingly associate more with adults as they grow (Clapham 1994). Adult right whale females that will neither forage nor mate migrate to the Península with their 1-yr old calves to wean them there (Rowntree *et al.* 2001, Sironi and Snowdon *in prep.*). This implies that there must be important benefits for yearlings to be weaned in this nursery ground.

North Atlantic right whales aggregate in large surface active groups during which males appear to compete for access to a single female (Kraus and Hatch 2001). Females are extremely selective when choosing mates. Females prevent males from copulating by staying belly up and keeping their anogenital region above the surface for prolonged periods, while males physically compete among themselves to copulate with the focal female when she rolls to breathe (Payne and Dorsey 1983, Payne 1995, Kraus and Hatch

2001). It is expected that juvenile right whales will practice adult sex behavior before they participate in these groups. It has been suggested that juvenile right whale females may spend more time than males in the vicinity of mother-calf pairs to learn appropriate maternal behavior (Payne 1995), but this has not been quantified.

Play behavior in young animals is considered important for the development of skilled movement, communication and social relationships (Fagen 1993). Play has been described in a variety of mammalian species such as house mice (Byers and Walker 1995), domestic cats (West 1974), pronghorns (Byers 1997), and primates (Owens 1975, Goodall 1986, Brown 1994, Pereira and Fairbanks 2002). In many species, locomotor play predominates in early life during critical periods of cerebellar and muscular development (Byers and Walker 1995, Byers 1998) and more interactive forms of social play arise later (Thompson 1998). In nonhuman primates, rates of social and nonsocial play decline consistently from late infancy or early juvenility through adolescence to adulthood (Fagen 1993). Among cetaceans, play has been documented mainly in odontocetes like the bottlenose dolphin (Connor *et al.* 2000) and the orca (Rose 1992, Baird 2000). Among baleen whales, there are accounts of play in right whales (Payne 1995) and in bowhead whales (Würsig *et al.* 1989).

Previous studies have described some aspects of juvenile behavior in baleen whales, *e.g.*, participation of juvenile North Atlantic right whales in surface active groups (Kraus and Hatch 2001), patterns of association in juvenile humpback whales (Clapham 1994), and growth and mortality in young gray whales (Sumich 1986, Sumich and Harvey 1986). However, no studies based on focal follows of individuals to date have focused on the behavior, social interactions, maturational changes and interspecific interactions of juvenile southern right whales at a nursery ground. Studying individuals for extended periods of time is important to address questions related to patterns of behavior and association in animals of different sexes and ages (Clapham 2000). Golfo San José at Península Valdés provides a unique setting to observe right whales of all age classes from shore without any apparent disturbance to their behavior.

In this paper we provide a general description of the behavior and social interactions of juvenile southern right whales at the nursery ground in Golfo San José. We provide behavioral accounts of juvenile right whales involved in play, feeding and sexual behavior. We compare the overall behavioral budget and patterns of association of juveniles to those of adults and mother-calf pairs, and describe seasonal changes in the social environment of right whales during the calving season. We discuss how the opportunities juveniles have in Valdés to learn and to practice effective behavior and social skills may prepare them to become successful adults. Understanding how juvenile right whales interact with their social and ecological environment at a site with relatively little human disturbance such as Golfo San José can be important to detect environmental degradation in the future.

MATERIALS AND METHODS

Study Site. Península Valdés is located on the Argentine coastline of the South Atlantic (Fig. 1). The coasts alternate between high cliffs and regions of broad beaches with gradually sloping sandy or pebbled bottoms. The Península is a large cape which encloses two bays: Golfo San José to the north and Golfo Nuevo to the south. Right whales concentrate in these two gulfs (Rowntree *et al.*, 2001) (Fig. 1). Golfo Nuevo has two towns on its shores, a flourishing whale-watching industry, an aluminum factory and commercial ship traffic. Golfo San José is a Provincial Marine Park that at present has little human disturbance. The research station and Observation Hut (42º25'S, 64º9'W) are located on its shores. The hut is built on a cliff-top overlooking the ocean at 45 m above sea level.

Subjects. Individual whales were identified by the unique pattern of callosities on their heads and by white marks on their backs (Payne *et al.* 1983, Payne and Rowntree 1984). Photographs (black and white prints and color transparencies) of juveniles were taken with a 75-300 mm lens. Drawings of their callosity patterns, back marks, scars and notches on pectoral fins and tail flukes were also used for individual identification. Sex was determined when the whales rolled belly-up and the anatomical differences in the anogenital configuration of females and males were visible to the observer (Payne and Dorsey 1983).

Kraus and Hatch (2001) classified juvenile North Atlantic right whales as individuals that are less than 10 yr old. However, in this paper the term "juvenile" refers to whales whose estimated age is one to four years (Rowntree *et al.* 2001). We preferred this more conservative approach because the minimum age at first calving in Valdés is 7 yr (Cooke *et al.* 2001), and because one North Atlantic right whale female is known to have given birth at age five. This indicates that right whale females can be reproductively active between ages four to six assuming a 1-yr gestation period (Best 1994).

The juvenile condition of a whale was determined in four different ways: (1) by identifying the individuals in their year of birth and thus knowing their age when resighted in later years; (2) by estimating their age from measurements of body dimensions taken on photographs and following the mean growth curve constructed by Whitehead and Payne (1981) for this population based on the head length to body length ratio; (3) by comparing the subjects' body size to nearby adult females (identified as such by the presence of an accompanying calf) whose mean total length for this population is 13.66 m (Whitehead and Payne 1981); or (4) by their evident small size. To analyze differences in behavioral development, juveniles of known and estimated age were classified into two age categories, yearlings and 2-to-4 yr olds. We grouped all 2 to 4 yr old whales into one category due to the uncertainty in assigning juveniles to a specific year of age when their year of birth was unknown.

Behavioral Sampling and data analysis. *Continuous focal sampling*. Behavior was recorded during the daytime by continuous focal-animal sampling (Altmann 1974, Martin and Bateson 1993, Mann 1999). Behavioral patterns were assigned to the mutually exclusive categories described in Appendix 1. Behavioral patterns were entered in real time into a Hewlett Packard 48GX calculator that was programmed to function as an event recorder. Duration (in sec) of each behavior pattern was automatically recorded. Date, time, whale identity and sex (if known), group size and age composition during social interactions, tide, sea state, weather conditions and distance to shore were also recorded. Given the difficulty of continually identifying individuals in surface active groups, some of these observations were recorded on audiotape and later transcribed. All whales that interacted with the focal subject during a focal follow were referred to as "secondary whales".

We used a 20X wide angle spotting scope mounted on a tripod to observe the whales. Focal subjects were selected by their proximity to the observation site, and they were followed visually to distances of up to 2 km. Subjects were abandoned when one (or both) of the following occurred: (1) they were too far to be identified and to record their behavior accurately; or (2) there were other juveniles in the vicinity to be observed after 90 min of continuous observation of the focal animal. This time limit was set because preliminary analysis showed that the number of behavior patterns recorded did not show a substantial increase after nearly 90 min of observation (approximately 75 % of all behavior patterns recorded in 81 focal follows were observed in the first 90 min). However, because rare behavior patterns may be observed only after longer observation sessions, focal follows were continued for as long as possible when no juveniles other than the focal subject were present in the area (see Mann 1999).

Behavioral patterns and categories. The behavior patterns recorded during focal follows are described in Appendix 1. Operational definitions in Appendix 1 were elaborated based on field observations from 1997 and 1999 and from the literature. Some specific patterns were combined into broader categories (*e.g.*, rolling, rocking, flipper slapping, lobtailing, tailing, spyhopping and breaching were grouped into the category "surface activity"). The behavioral categories used for the analysis were: rest; social rest; travel slow; travel medium/fast; social travel; gull attacks; surface activity; turning toward; turning away; active interactions; passive interactions; belly-to-belly; belly up; and underwater. Play was not recorded as a single behavior but rather as a sequence of several motor patterns. We followed Bekoff and Byers (1981) to define play as "all motor activity performed postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing. If the activity is directed toward another living being it is called social play." We restricted "living being" to southern right whales. We followed Fagen (1981) to define object play as "divertive interactions with an inanimate object (…) including exploratory manipulation." Sexual behavior was considered to occur in groups where the penis of one or more males was visible (erections), or body postures involving potential physical contact between the genital slits of two or more whales were repeated during the interactions.

Spatial and social relationships. Relative spatial relationships among individuals, measured by "whale lengths" (WL, the body of the focal whale being used as a scale to measure distance between animals), were recorded on paper as they changed during the interactions. The distance between animals was divided into three discrete categories: (1) less than 1 WL, (2) 1 to 5 WL, and (3) more than 5 WL. These categories were used to determine the proportion of solitary *vs*. social time. A whale was considered to be "social" when there was at least one other whale at a distance of 5 WL or less from it; otherwise, it was "solitary." An exception to this rule were the two members of a mother-calf pair: the pair was social when a third whale was less than 5 WL from either of them. The term "group" refers to two or more whales at 5 WL or less from each other (except for cows and their calves). The 1 WL limit was chosen as a distance where physical contact could occur. The 5 WL limit was chosen to ensure that whales were not in visual contact with each other underwater, although accoustic contact was likely.

The "direction" of social interactions was defined in terms of "actors" and "recipients" (*cfr*. Mann and Smuts 1999). For example, if whale A used its flippers to rubb whale B, whale A was defined as the "actor" ("active interaction") and whale B as the "recipient" ("passive interaction") of the interaction ("rubbing"), and the interaction was defined as "asymmetric". Social interactions in which there were no obvious actors and recipients were defined as "symmetric" (*e.g.*, two whales resting or traveling five whale-lengths or less from each other).

Instantaneous scan sampling. We surveyed a 3.8-km long and 2-km wide strip of coast by instantaneous scan sampling (Altmann 1974) every hour. Scans allowed us to assess the general activities of other animals besides the focal whales as well as to determine whether other known subjects were present. During scans, we recorded the number and the age class of all whales sighted (mother-calf pairs, adults, juveniles and animals of unknown age), their overall behavior (surface activity, travel, rest, underwater), their sociability (solitary or social), and whether or not they were attacked by kelp gulls (*Larus dominicanus*) (see Rowntree *et al*. 1998). We also counted kelp gulls at roosting sites and mussel beds in the same bay. This was done to estimate the number of gulls that could potentially attack the whales. Sea state, wind speed and direction, tide and cloud cover were also recorded at the beginning of each scan.

Data analysis. The proportion of time that focal subjects spent under the different behavior patterns during focal follows was calculated. The proportions were normalized by the arc sin of the square root, and the transformed data were used for statistical analysis. However, real time percentages are given in the results. Means ± standard deviation are given in the text. Comparisons of the transformed time proportions were done with the Student t-test. Statistical tests were carried out using SPSS version 11.0.1

for Windows (SPSS Inc., 2001). Tests were two-tailed and the level of significance was set at α = 0.05.

Some behavioral patterns were added to the program in the event recorder for focal follows obtained after 1999. Therefore, individuals from the 1999 field season are not included in some behavioral comparisons, and consequently, sample sizes (and degrees of freedom) vary in the following analyses. Descriptions of the overall behavior of juveniles were made based on focal follows of 191 individuals. Sex comparisons of juvenile behavior were made between 29 females and 42 males (or 26 females and 35 males when the juveniles of known sex from 1999 were excluded). Age comparisons were made between 58 yearlings and 25 juveniles that were between 2 and 4 yr of age. The sample sizes used for other comparisons are given in the results.

Within-season observations of resighted individuals were pooled and treated as one sample for that season for each resighted subject to avoid pseudoreplication (Mann 1999). Focal follows obtained in different years were considered to be independent. It is likely that some known focal subjects were followed in more than one occasion without positive identification as a resighted individual. The identity of whales during the hourly scans was not recorded, and some whales were counted on more than one scan throughout the same day. This introduces the problem of non-independence between scans during the same day. However, given the large sample size and the prolonged time period of data collection (see following section) we consider that the effect of non-independence in the interpretation of the results from the analysis of scans is minimal.

RESULTS

Data collected

A total of 1,115 scans were done in 1,013.5 h of observation in 156 d during the 1999-2001 nursing seasons (Aug-Nov). From 10,331 whales counted in the scans (including resightings), 58.3% were mothers and calves, 17.5% were adults, 16% were juveniles, and 8.2% were whales whose age class could not be determined. There were on average 9.3 whales present in the study site at any one time (SD = 3.8, range = 0 – 37). During 1,152.5 h of observation effort in 1997 and 1999-2001, 191 individual juvenile whales were followed visually in 260 focal animal samples during 283.4 h of continuous observation. The mean duration of follows was 65.4 min (SD = 49.2; range = 7.3 – 358.4). Approximately 2,700 photographs were used to identify individuals and to take body measurements to estimate the age of juveniles. Known individuals were resighted on as many as 13 different days throughout the same season over a maximum period of 68 d.

Sex and age distribution of the subjects

We did not determine the sex of individuals during scans. During focal samples, 29 juvenile females, 42 males, and 120 whales whose sex could not be determined were observed. The age of juveniles was known or estimated (as described above) for 16 females (x = 1.3 yr, SD = 0.6, range = 1 – 3), 24 males (x = 1.8 yr, SD = 1.03, range = 1 –

4) and 43 whales of indeterminate sex (x = 1.4 yr, SD = 0.65, range = 1 – 4). We used seven known-aged juveniles for which we obtained full body photographs to evaluate the reliability of estimating their age by measuring the proportion of head length to body length on photographs (Whitehead and Payne 1981). The true age and estimated age of six juveniles (85.7%) were the same, while in one yearling the estimated age was 2 yr.

Focal whales whose age was not known or could not be estimated from photographs were assumed to be juveniles by their evident small size. We took a conservative approach when classifying large juveniles as such. Large juveniles that possibly were around 4 yr of age might have been excluded as subjects in focal samples because of the uncertainty in their age class. Hence, by selecting smaller whales for behavioral observations the mean estimated age of focal subjects was low. Similarly, during scans, young whales of relatively large size could have been assigned to the adult or the indeterminate age categories, thus artificially decreasing the proportion of juveniles in the population during the scans.

Overall behavior of juveniles

Locomotory behavior patterns. The time juvenile females and males spent within most behavioral states showed no significant sex differences (Fig. 2). When added together, slow solitary travel and social travel were the most common behavior for females (39.2 ± 16.8 %) and males (35.5 ± 22.4 %). The overall resting time (solo and social rest) represented 18 ± 17.5 % and 22.3 ± 15.6 % of the daily behavioral budget of females and males, respectively. The patterns grouped as "surface activity" represented 20.1 ± 15.3 %

and 21 ± 22.3 % of the daily behavioral budget of juveniles females and males, respectively. Females spent significantly more time than males belly up (t = 3.13; df = 69; P = 0.003) and as passive recipients during interactions (t = 2.3; df = 59; P = 0.024), and females turned away from secondary whales more frequently than did males (t = 2.59; df = 69; P = 0.012) (Fig. 2).

Play behavior. Behavior that could be described as play was observed in 26 focal follows of 16 females (55.2 % of 29 known females) and in 23 focal follows of 22 males (52.4 % of 42 known males). Play is a sequence of several motor patterns rather than a single behavior pattern (*e.g.*, traveling). For this reason, the onset and end times of play bouts were difficult to determine, and duration of play was not recorded. Instead, the percentage of individual females and males that played during focal samples was calculated (Fig. 3). The occurrence of solitary, social and/or object play was not mutually exclusive within focal samples, *i.e.*, two types of play could occur during the same focal sample. As a consequence, total percentages for each sex in Fig. 3 add up to more than 100 %.

Solitary play was observed in 11 females and 11 males. Solitary play was characterized by sequences of motor patterns including rolling, flipper slapping, lobtailing, tailing, breaching, spyhopping and rocking. These motor patterns were frequently interspersed with short erratic travel and even with brief (2-3 min) periods of rest. While tailing during play bouts, in contrast to adult whales, juveniles held their tails up in the air in an unstable fashion (the tail "falling" to the sides and being held up again). Flipper slapping occurred most often while whales lay on one side and repeatedly slapped the water surface with the ventral side of one flipper, producing a loud noise. In one instance, a juvenile male was seen slapping the dorsal side of both flippers at the same time against the water surface while lying belly up.

A particular type of solitary play involved objects. In four separate instances, two females, one male and one juvenile whose sex could not be determined played with floating fronds of kelp. On another occasion, one male played with a floating plastic bag approximately 1 m long. The motions involved during object play were similar in all cases. Juveniles swam underneath the floating objects and placed them on their rostrums, sliding the kelp or the bag along their heads, blowholes and backs. These movements were repeated up to tens of times. One female spent at least 70 min uninterruptedly playing with kelp fronds while rolling at the water surface. She placed the kelp on her head and also manipulated the kelp with both flippers while she was belly up at the surface. She used her flippers to pass the kelp from side to side on her chest. Three occasions when juveniles were seen playing with kelp occurred after two days of strong N and W winds (25-35 mph) that probably cut off the kelp from the sea bottom and brought it to the surface near the observation site.

On September 25, 2002, a male yearling named Garra got entangled in the mooring chains of a whale-watching boat in Golfo Nuevo at Península Valdés. We first identified Garra as a calf with his mother on August 25, 2001 at the study site in Golfo San José. When Garra got entangled, he was at least 13.2 mo old. It is likely that Garra was playing with the chains when he got entangled. Garra was rescued and released by the local people. Despite having a distinctive white mark on his back that makes him relatively easy to identify, one year after his release he has not been resighted.

Social play (involving the focal subject and at least one secondary whale) was observed in 11 females and 10 males. Juvenile females played with mother-calf pairs significantly more often than males, whose most frequent play partners were other juveniles (Fisher Exact test, df = 1, P = 0.033). Eight of the females (72.7 %) played with mother-calf pairs and six (54.5 %) with juveniles. Of the eight females that played with mother-calf pairs, seven interacted primarily with the calf. In six of these follows, the juvenile females initiated contact with the pair, while in one occasion it was not clear who initiated the interaction. In the eight encounters, the mother in the pair ended the interactions by turning away from the juvenile female and the calf followed the mother. Juvenile females playing with calves engaged in mutual rubbing with the flippers, milling around each other, and rolling at the surface while maintaining physical contact. In one instance, a yearling female and a very small calf played in this fashion for at least 30 min. The calf even breached and landed on the mother's back at least five times. The calf's mother stayed at one body length from the young whales, resting or slowly swimming in circles around them before turning away to end the encounter with the juvenile. On a different day, another juvenile female approached five mother-calf pairs over the course of 1 h and apparently played with at least three of these calves.

Of 10 males that engaged in social play, only one (10 %) played with a mother-calf pair and the remaining nine (90 %) played with other juveniles. In the first case, after 25 min of active interactions of the juvenile male toward the mother-calf pair, the mother slashed her tail horizontally at the surface before turning away from the male to end the encounter.

The sex of seven of the secondary juveniles that played with focal juvenile males was determined: five were males and two were females. Play among males was characterized by repeated mutual pushing with the head on the flanks and tailstock, chasing each other in circles, rolling at the surface, breaching and flipper slapping. One play session involving two males and one juvenile whose sex could not be determined lasted for at least 170 min.

Sex differences in play behavior were evidenced by two types of interactions that were only observed among males: “tail tussling” and “dragging”. During tail tussling two males that were on a diagonal to each other at the surface, crossed their tail flukes and pulled each other from the tail. During dragging two whales were belly-to-belly and head-to-tail. The whale that was underwater and belly up grabbed the tail stock of the other whale with both flippers and dragged it backwards by pulling it from its tail. Tail tussling and dragging were observed in three and two juvenile male focal follows, respectively.

Sexual behavior. Juveniles of both sexes participated in groups where sexual activity occurred. The posture belly-to-belly was considered separately from other surface activities to assess the time females and males were in a position where potential genital stimulation (and potential mating) could have occurred (although actual copulations in this posture are impossible to see from shore). The time that 13 females and 24 males were in this posture with secondary whales was not significantly different ($t = 0.34$; $df = 35$; $P = 0.74$). However, juvenile females ($N = 29$) spent significantly more time belly up than males ($N = 42$) ($t = 3.13$; $df = 69$; $P = 0.003$). Juvenile females could be practicing this posture that appears to be relevant to avoid unwanted copulations when females engage in surface active groups as adults.

Sexual behavior was observed in 11 follows of eight juvenile females that appeared to be the focal individual in the groups (see Kraus and Hatch 2001). The mean number of individuals in these groups was 3.3 ± 0.9 (range = 2-5; N = 11), and the mean age of the focal females (when known) was 1.5 ± 0.5 yr (range = 1 – 2; N = 6). Adult males were present in at least seven groups (63.6 % of 11 groups) and male juveniles were the only males present in three groups (27.3 %). Erections of at least one male were observed in six groups and actual penetration of an erect penis in the genital slit of the focal female was seen in three cases: the three males were of adult size. In one instance, one adult and one juvenile male explored the genital slit of a belly-up juvenile female with their penises simultaneously. Only the adult male was seen copulating, after which the group (containing the focal female and three males) separated after at least 3 h of group activity. Four focal females repeatedly turned away from the males, who followed them and intercepted the females' travel to stop them. One of these females turned away from two juvenile males and traveled at the highest swimming speed observed during the present study. The males reached her and stopped her, and group activity continued for at least 2 h until sunset. The female persistently stayed belly up possibly avoiding the males' attempts to copulate.

Sexual behavior was observed in eight focal follows of seven juvenile males. The mean number of individuals in these groups was also 3.3 ± 1.4 (range = 2 – 6; N = 8), and the mean age of the focal males (when known) was 2.3 ± 1.5 yr (range = 1 – 4; N = 4). Female whales were present in three groups (37.5 %) and in the remaining five groups

(62.5 %) only male whales were observed. Erections during heterosexual interactions were seen on two occasions when the focal males interacted with one juvenile and one adult female. We observed homosexual behavior among juvenile and adult males. Three focal juvenile males displayed erections while interacting with other juvenile males. An adult male in a rolling group with at least six whales inspected the genital slit of one juvenile male with his penis. One juvenile male that displayed an erection (but apparently did not copulate) in the group that separated after an adult male copulated with a juvenile female, was seen 10 min later displaying an erection while interacting with a male calf. One juvenile male that displayed heterosexual behavior with a juvenile female was involved in homosexual behavior 80 min later with another juvenile male. The same juvenile female turned away from the two males and rested at the surface at a distance of 150 m from the two males, who displayed erections while interacting with each other.

Feeding behavior. Six juvenile right whales (two females and four whales of unknown sex) were observed feeding during focal follows. Feeding bouts lasted on average 133 ± 117 min (range = 50 – 360) and the mean estimated distance to shore was 733 ± 1,119 m (range = 100 – 3,000). Two juveniles fed alone while other whales in the vicinity (30 – 500 m) did not feed. Two juveniles fed simultaneously with one other juvenile and one adult at distances of 10 to 400 m between them, swimming slowly at the surface with frequent changes in direction in an area of 200 – 400 m in diameter. Another juvenile fed in a similar way for at least 140 min at a distance of 10 – 200 m from a mother-calf pair, while the mother in this pair also fed. In an unusual occurrence for Península Valdés, a one-year old female was seen feeding together with 20 to 30 whales at a distance of 3 km from shore along a line that stretched for approximately 5 km parallel to shore. Feeding activity on this day occurred at and below the water surface and lasted for at least 6 h. Plankton samples collected contained mostly *Euphausia* sp. and calanoid copepods. We observed feeding behavior among juveniles as early as Aug 11 and as late as Oct 24 during the study period.

One right whale cow accompanied by her female yearling fed on Aug 17 and then again on Aug 19. On Aug 17 the mother fed for at least 80 min while the yearling followed her at less than one whale-length. At the same time, one adult fed at 200 – 300 m from them, while a group of 80 – 100 dusky dolphins (*Lagenorhynchus obscurus*) fed in the same area. On Aug 19 the same right whale cow fed for at least 50 min, but the yearling separated from her and swam at a distance of at least 1 km before returning to the mother. The yearling was not observed feeding on either day.

Solitary vs. social individuals

We compared the overall behavioral budgets (travel, rest, surface activity and underwater) of solitary and social juvenile whales. During focal follows, juveniles spent 55.3 % of their time alone and the remaining 44.7 % interacting with whales of all age classes. This distribution between solo and social time was very similar for females (56.5 % and 43.5 %, respectively) and males (54.1 % and 45.9 %, respectively).

We compared the behavior of 28 juveniles that were solitary for 22.9 h and 49 juveniles that were socializing for 45.7 h during entire focal follows (Fig. 4). Solitary juveniles spent significantly more time resting (t = 2.02; df = 75; P = 0.046) and underwater (t = 2.75; df = 75; P = 0.007) and less time in surface activity (t = -2.77; df =

75; P = 0.007) than social juveniles. No difference was found in the overall time spent traveling (t = 0.78; df = 75; P = 0.44) between the two groups. However, solitary juveniles traveled at slower speeds than social juveniles (t = 4.37; df = 75; P < 0.001), who spent approximately half of their travel time (52.2%) moving in close proximitiy (within 1 WL) of at least one other whale.

The behavior of 25 juveniles that were both solitary and social at different times during the same focal follow was observed for 37.1 h (Fig. 5). The differences in behavioral budgets follow a similar pattern as above. When solitary, juveniles spent significantly more time traveling (paired t = 3.74; df = 24; P = 0.001) and resting (paired t = 2.58; df = 24; P = 0.017) and less time in surface activities (paired t = -7.29; df = 24; P < 0.001) than when they were social.

We determined the sex of seven females and 11 males of the 28 juveniles that were solitary during entire focal follows (total observation time for the 18 solitary females and males = 22.2 h) (Fig. 6a). Solitary females spent significantly more time resting than solitary males (t = 2.35; df = 16; P = 0.032), but they did not differ in the time spent traveling (t = -1.66; df = 16; P = 0.12), surface active (t = -0.77; df = 16; P = 0.45) or underwater (t = -1.1; df = 16; P = 0.29). Similarly, the behavior of 8 females and 14 males of the 49 juveniles that were social during entire follows was observed for 16.9 h (Fig. 6b). No significant differences between social females and males were found in the time they spent under the four behavioral patterns considered for this analysis.

The age class of the nearest neighbor (the nearest whale that was beyond a 5 WL radius from the focal juvenile) was recorded in 61 occasions while juvenile females were solitary (Fig. 7). The most frequent nearest neighbor to juvenile females were mother-calf pairs (50.8%), followed by other juveniles (27.9%) and adults (21.3%). This distribution is significantly different from the expected based on the percentage of each age class at the study site ($\chi^2 = 6.46$, df = 2, P = 0.04). The most frequent nearest neighbor to solitary juvenile males in 50 occasions were also mother-calf pairs (42%), followed by other juveniles (34 %) and adults (24%) (Fig. 7). This distribution was highly significantly different from the expected ($\chi^2 = 13.61$, df = 2, P = 0.001). The observed proportion of juvenile nearest neighbors to juvenile males was over two times higher than the expected based on the proportion of juveniles at the study site (16 %).

Social interactions

Sixty-three focal animal samples (86.7 h) of 29 females and 66 focal animal samples (77.5 h) of 42 males were used to describe and compare the social behavior and interactions of juveniles. Because the data collection changed slightly during the study (behavioral patterns were added after the 1999 field season), sample sizes vary in the following analyses.

Juveniles of both sexes spent most of their socializing time with other juveniles, followed by mother-calf pairs and adults (Fig. 8). During focal follows, juvenile females distributed their social time more evenly than juvenile males, who spent 70.1 % of their socializing time with age peers. Juvenile females spent significantly less time with other juveniles (t = -2.13; df = 59; P = 0.037) and more time with adults (t = 2.27; df = 59; P = 0.027) than juvenile males. Although females spent more time with mother-calf pairs than males, this difference was not statistically significant (t = 1.38; df = 59; P = 0.17).

There were differences by sex in who initiated, maintained and terminated the interactions with other whales, and in the role (active *vs*. passive, see Appendix 1) of females and males during social encounters.

Initiation and termination. During focal follows of juvenile females and males, the initiator (the whale that actively turned toward another whale to initiate an interaction) was recorded on 61 and 51 occasions, respectively. The termination of interactions was less evident than the initiation. In several instances, the interactions continued beyond the duration of the focal sample, and termination could not be recorded. The terminator (the whale that actively turned away from another whale to end an encounter) was recorded on 39 and 25 occasions during follows of females and males, respectively.

The proportion of interactions initiated by juvenile females and males with mother-calf pairs, adults and other juveniles was significantly different from the expected based on the age class distribution (Fig. 9). The proportion of initiations by juvenile females with mother-calf pairs (57.9 % of all interactions inititated by females) did not differ from the expected, although females initiated significantly more interactions with other juveniles than expected ($\chi^2 = 6.8$, df = 2, P = 0.033). In contrast, juvenile males initiated four times more interactions with other juveniles (64.9 %) than expected, and fewer interactions with mother-calf pairs than expected ($\chi^2 = 65.5$, df = 2, $P < 0.001$). Female and male juveniles initiated relatively few interactions with adult whales (10.5 % and 18.9 %, respectively).

The pattern of interactions initiated by secondary whales (whales that interacted with the focal subjects during follows) with juveniles was also different from the expected (Fig. 9). The distribution of initiations by secondary whales was significantly different from the expected for females ($\chi^2 = 38.1$, df = 2, $P < 0.001$) and males ($\chi^2 = 42.5$, df = 2, $P < 0.001$). Mother-calf pairs rarely initiated contact with juvenile females and never with juvenile males. From all the interactions initiated by secondary whales with juvenile females, nearly half of them were initiated by adults (52.2 %). When the sex of these adults could be determined, 75 % (9 out of 12) were males. The remaining interactions (43.5 %) initiated with focal juvenile females were initiated by other juveniles. Most interactions (78.6 %) initiated with focal juvenile males were initiated by other juveniles, and the remaining by adult whales (Fig. 9).

Mother-calf pairs terminated most interactions with juvenile females and males (19 out of 28 interactions involving mother-calf pairs), and juveniles of both sexes terminated most encounters with adults (8 out of 10 interactions involving adults). Interactions with age peers were more frequently terminated by juvenile females (11 out of 16 interactions involving secondary juveniles) than by juvenile males (5 out of 10).

Direction of social interactions. There were sex differences in the role juveniles played during asymmetric interactions (see Appendix 1). Juvenile females assumed a predominantly active role (*i.e.*, actively initiating encounters by turning toward secondary whales, circling around them, rubbing them, following them when they turned away, *etc.*) when they interacted with mother-calf pairs. Juvenile females spent significantly more time playing an active role during encounters with mother-calf pairs (56.3 % of all the time they spent as actors) than with juveniles (31.3 %) or adults (12.3 %) (ANOVA, $F_{(2,72)} = 5.26$, $P = 0.007$) (Fig. 10). When it was possible to discriminate whether the focal juveniles were interacting primarily with the cow or with the calf in a pair, juvenile females interacted with calves significantly more than juvenile males (t = 2.62; df = 59; P = 0.011) (see Fig. 11).

On the other hand, juvenile males assumed a predominantly active role during interactions with age peers. Juvenile males spent significanly more time as actors with other juveniles (61.7 %) than with mother-calf pairs (37.1 %) or adults (1.2 %) (ANOVA, $F_{(2,105)} = 7.5$, $P < 0.001$) (Fig. 10). The time males spent as actors during interactions with other juveniles was significantly more than the time they spent as recipients (t = 2.42; df = 35; P = 0.021).

The roles of juvenile females and males were different during their encounters with adult males. Juvenile females spent significantly more time than juvenile males as recipients during interactions with adult males (t = 2.13; df = 59; P = 0.038). This suggests that the interactions of juvenile females with adult males may be a consequence of the active role that the adult males play in initiating and maintaining interactions with juvenile females *vs*. males.

Behavioral comparisons by age

Within the juvenile age class. The age of 83 juveniles was known or could be estimated from measurements on photographs or from direct body size comparisons with adult cows. Fifty-eight subjects (12 females, 15 males and 31 juveniles whose sex could not be determined) were 1 yr old and 25 (4, 9 and 12, respectively) were between 2 and 4 yr old. Behavioral comparisons were made between these two age categories. The overall locomotory behavior (rest, travel, surface activity) of females and males considered together did not differ between the two age categories. However, 2-4 yr old juveniles spent significantly more time than yearlings socializing in active (t = 2.13; df = 81; P = 0.036) and passive (t = 2.08; df = 81; P = 0.04) interactions with other whales.

A within-sex comparison showed that 2-4 yr old males spent significantly more time than yearlings traveling within 5 WL of other whales ("social travel") (t = 2.32; df = 18; P = 0.032), in active interactions (t = 2.71; df = 22; P = 0.013), and also belly-to-belly with other whales (t = 2.18; df = 17; P = 0.04). Due to the small number of 2-4 yr old female focal follows we did not determine the significance of these differences for females.

Between age classes. We analyzed the scans to compare the overall behavior and interactions between age classes (Fig. 12). Travel was the most frequent locomotory behavior of mother-calf pairs (47.1 % of all pairs observed during the scans were traveling) and surface activity was the most frequent among juveniles (42.3%). Adult whales were most frequently observed in rolling (surface active) groups (44.3 %) whereas mother-calf pairs were virtually absent from these groups (Fig. 12).

We observed 2,576 social interactions among whales of all age classes during the scans. The majority of the interactions involved whales of the same age class. Adults, juveniles and mother-calf pairs interacted with age peers in 87.8 %, 75.4 % and 67.3 % of their social encounters, respectively. Adult right whales were the most social age class (69.3 % of adults observed were socializing) and mother-calf pairs were the most solitary (86 % of all pairs observed were alone) (Fig. 13). Juveniles distributed their social and solitary time more evenly (54.7 % and 45.3 %, respectively) (Fig. 13).

Seasonal changes in social environment, behavior and interactions

The mean number of whales of each age class per scan varied throughout the season (Fig. 14) and therefore the social environment of the whales changed. The average number of mother-calf pairs per scan was lowest in early Aug (1.1), it peaked in late Sep (4.1) and then decreased until late Nov (1.6). The number of adult whales peaked in early Aug (2.8 adults per scan) and then decreased. By late Oct, fewer than one adult per scan was counted, and by mid-Nov adults were virtually absent from the study site. The number of juveniles remained stable at two whales per scan from mid-Aug until late Sep and then decreased. Juveniles stayed longer than adults at the study site, although by late Nov most juveniles had left the area.

The percentage of time that juveniles spent each month traveling, resting or underwater was similar from Aug to Nov (Fig. 15). Rolling group activity was recorded separately from other surface activities to determine if there were seasonal differences in the time juveniles spent in groups where they could potentially learn and practice sexual behavior. The time juveniles spent in rolling groups increased throughout the season, from 4.3 % of their socializing time in Aug to 8.9 % in Nov. No apparent changes in the overall time juveniles spent with each age class were recorded throughout the season (Fig. 16), although relatively more interactions with other juveniles and fewer interactions with adult whales were seen in Nov than in the previous three months.

Interactions with other species

Kelp gulls. Interactions between right whales and kelp gulls (*L. dominicanus*) were observed throughout the study. Kelp gulls land on the whales' backs (a "gull attack") to eat their skin and blubber, and the whales react by flinching and swimming away (Rowntree *et al.* 1998). During 1,077 hourly scans, we counted 69,713 gulls at the intertidal zone in the study site and observed 652 gull attacks on whales of all age classes (x = 64.7 gulls per scan, SD = 53.1, range = 0 – 340). We observed 187 gull attacks on juvenile right whales during 238 h of focal follows. The most obvious effects of the attacks on the behavior of juveniles were the interruption of resting bouts and in some cases, disruption of social interactions occurred after the attacks.

Attacks on mothers and calves observed during scans were recorded as occurring "on the pair" and not on the individual member of the pair. As a consequence, mother-calf pairs are counted as one "whale unit" (and not as two individual whales) for the purposes of calculating the percentage of attacks that were aimed at all whale age classes. We compared the observed number of gull attacks on each age class to the expected number based on an even distribution of attacks on all age classes. The distribution of gull attacks observed on each age class was significantly different from the age class distribution of whales at the study site ($\chi^2 = 426.2$, df = 3 , $P < 0.001$) (Fig. 17). Mother-calf pairs (41.2 % of all whales counted) were the most frequent target of gull attacks (80.8 % of all attacks observed during scans occurred on mother-calf pairs). Juvenile whales (22.6 % of all whales counted) were the target of 8.9 % of all gull attacks observed during scans. The percentage of gulls present at the study site that were observed attacking the whales at any one time was minimum (1 % on average).

Over one half of the attacks on juvenile whales during focal follows occurred when juveniles were alone (59 % of the attacks for females and 65.1 % for males). However, the rate of attacks per hour was highest when juveniles were interacting with mother-calf pairs (6.2 and 4.3 attacks / h for juvenile females and males, respectively, compared to 2.2 and 2.5 attacks / h when juveniles were solitary) and lowest when they were in groups containing adult whales (1.9 and 0 attacks / h). The nearest neighbor to solitary focal juveniles was recorded on 50 occasions during gull attacks. Mother-calf pairs were the nearest neighbor in 53 % and 28 % of the follows of solitary juvenile females and males, respectively, when attacks occurred, followed by other juveniles (22 % and 28 %), adults (19 % and 22 %) and whales whose age could not be determined (6 % and 22 %).

Dusky dolphins and southern sea lions. Dusky dolphins (*L. obscurus*) and southern sea lions (*Otaria flavescens*) were regularly seen at the site throughout the study period (*e.g.,* dusky dolphins were seen on at least 55 days), but few physical interactions with right whales occurred. Dolphins (in groups of 5 to 20 animals) and sea lions (2 to 3) approached juvenile whales during six and two focal follows to distances of less than 5 m. The interactions lasted 12.4 min on average (SD = 6, range = 4 – 20). On one occasion a resting juvenile began to roll at the surface after two sea lions repeatedly circled around the whale's head. The whale returned to a resting posture 3 min later when the sea lions left. In the remaining seven interactions, the whales were in locomotor activities (solitary or social) and no obvious changes in their behavior could be attributed to the proximity of the other species.

DISCUSSION

The percentage of juvenile southern right whales (16 %) over the total whales counted from shore was low compared to the expected from a growing population (*cfr*. 28.9 % of whales identified in Golfo San José from aerial surveys, Payne 1986; 26-31 % in North Atlantic right whales, Hamilton *et al.* 1998). The majority of whales counted were mother-calf pairs who tend to swim close to shore in shallow water (Payne 1986). Scans were restricted to a maximum distance of 2 km from shore (the reliability of behavioral observations decreases at longer distances), but many whales (most likely, juveniles and adults) were seen beyond the 2-km limit. It is possible that the true proportion of juveniles and adults in the population was underestimated in the shore-based scans.

Overall behavior

Play behavior. Juvenile females and males did not differ in the overall time they spent in locomotory behavior such as travel and surface activities. When solitary, most surface activities resembled solitary locomotor play as described in other cetaceans (bottlenose dolphin, Mann and Smuts 1999, Connor *et al.* 2000; orca, Baird 2000) and in juvenile primates (Fagen 1993, Fairbanks 1993b). Frequent patterns included rolls, breaches, tailslaps and flipperslaps, which are aerial behavior patterns also described for orcas

(Baird and Dill 1995), bowhead (Würsig *et al.* 1989, Würsig and Clark 1993) and humpback whales (Whitehead 1985) at play. It is possible that these locomotor behavior patterns may influence neural and muscular development of the young whales, as has been described in young rodents and cats (Byers and Walker 1995, Byers 1998).

Object play is common over a wide taxonomic range (*e.g.*, turtles, Burghardt et al. 1996; ravens, Heinrich and Smolker 1998; carnivores and primates, Brown 1994). The kelp play described here is strikingly similar to the log play observed in bowhead whales (Würsig *et al.* 1989), play with leaves of lettuce in a captive baby Asian elephant (K. Payne 1998), and with seagrass in bottlenose dolphin infants (Mann and Smuts 1999). The main function attributed to object play in predatory animals is that it may serve as practice for hunting behavior (Hall 1998). Although this interpretation does not apply to right whales (who are essentially grazers), juveniles played with kelp in Valdés. Play may increase juvenile exposure to accidents and natural calamities (Thompson 1998), especially if juvenile right whales redirect object play toward ropes or chains to mimic the potentially pleasurable sensation (Würsig and Clark 1993, Payne 1995) of rubbing their bodies against kelp. It is likely that this is what caused the male yearling Garra to get entangled in the mooring chains of a whale-watch boat in Golfo Nuevo.

Juvenile right whale females possibly derive benefits from practicing maternal behavior in Valdés. Natal attraction was more evident among young females, who played with calves more often than did males. Similarly, nulliparous bottlenose dolphin females are more likely to escort newborns than are experienced females, and males rarely interact with calves, supporting the "learning to parent" hypothesis (Mann and Smuts 1998, 1999). Young female vervet monkeys show allomaternal behavior at a much higher rate than males (Fairbanks 1993a) and young female African elephants baby-sit more often than males (K. Payne 1998).

Juvenile males played more frequently with other juvenile males. Chasing, wrestling, and energetic body movements accompanied by context-specific signals all constitute play in animals (Fagen 1993, Byers 1998). It is difficult to discern play signals in whales such as the stereotypical signals that label play in canids (Pellis and Pellis 1998) and in young pronghorn males (Miller and Byers 1998). Hence, it is possible that some bouts of social play in juvenile right whales were in fact sexual or aggressive behavior, or even temper tantrums. However, during these encounters we did not observe erections nor any apparent aggressive use of callosities as described for adult males during sexual competition (Payne and Dorsey 1983). Thus, we assume that social play occurred in juvenile right whales, and juvenile males possibly tested their strength against each other during these encounters.

Sexual behavior. Mating in right whales occurs in surface active groups (SAGs) in which there are usually one focal female and several competing males (Kraus and Hatch 2001). These groups are frequent in Valdés (Payne 1986). Juvenile southern right whales spent 6.2 % of their time in SAGs. The mean number of whales (3.3) in groups where a juvenile female was the focal animal mirrors that observed in North Atlantic right whales (3.4, Kraus and Hatch 2001). Juvenile females spent significantly more time than males with their genital area in the air and turning away from males. These behavioral patterns are typically displayed by adult females to avoid unwanted copulations in SAGs (Payne and Dorsey 1983, Kraus and Hatch 2001). Nonconceptive cycles are likely to be common among juvenile female odontocetes who can practice mating strategies before actual pregnancy, although no such evidence exists in baleen whales (Whitehead and Mann 2000).

Juvenile males were observed displaying erections in SAGs but, contrary to adults, they were never seen copulating with a female, possibly because they do not yet have the skills or the strength to displace adult alpha males from the best positions to mate (Kraus and Hatch 2001). The participation of juveniles in SAGs was relatively more frequent late in the season, when fewer adults were present in Valdés and SAGs may have been composed primarily of juvenile whales. Young male chimpanzees copulate with females perhaps to practice sexual behavior during the phases of the females' cycle when adult males show little interest in them and are thus highly tolerant (Goodall 1986).

As in other baleen whales (*e.g.*, bowhead whales, Würsig and Clark 1993, grey whales, Bagemihl 1999) most homosexual behavior in right whales was observed (or was more evident) among males. No evidence of kin selection or reciprocal altruism in mating strategies exists yet for male right whales (Kraus and Hatch 2001). Kraus and Hatch (2001) suggested that the main function of male-only SAGs involving sexual behavior may be to develop and assess their ability in courtship activity by practicing upon one another. Sex differences that are part of adult right whale behavior (and that may reflect differential life-history strategies) begin to be established early in the whales' lives, as occurs in immature chimpanzees and bonobos (Goodall 1968, 1986, Hashimoto and Furuichi 1994).

Feeding behavior. Although sporadically, right whales feed at Península Valdés. Feeding behavior in juveniles followed the patterns described by Mayo and Marx (1990) for North Atlantic right whales. We observed juveniles, adults and cows feed. This indicates that when plankton is present, its density allows for whales of all age classes to forage at Valdés with no aparent age class segregation in feeding behavior as reported in bowhead whales in the Beaufort Sea (Würsig *et al.* 1989) and in humpback whales off Virginia (Swingle *et al.* 1993). However, there is little food available for the whales at Península Valdés (Payne 1986), and foraging does not appear to be a major advantage for right whales to migrate there. The observation of a yearling female that did not forage while her mother fed for over 2 h on two separate days may suggest that the yearling was satiated from nursing.

Social interactions

Juveniles spent nearly half of their time in Valdés socializing. Most surface activities occurred during social encounters, while resting was frequently a solitary behavior (*cfr.* Clark 1983). The time juveniles spent alone decreased with age, as observed in juvenile humpback (Clapham 1994) and North Atlantic right whales (Hamilton 2002). Juveniles, especially males, interacted primarily with age peers. The patterns of contact initiations and nearest neighbors indicate that juvenile males seek and actively maintain the company of other juveniles, showing a preference for partners of similar developmental state. If behavioral development continues at a smiliar rate, these partners may continue to be preferred over the course of their adult lives (Thompson 1998). Juvenile North Atlantic right whale males continue this process of increasing associations until adulthood, suggesting that males may form alliances presumably to increase mating success (Hamilton 2002). Male bottlenose dolphins form such alliances and cooperate to herd females (Connor *et al*. 2000). It has been suggested that long-term social bonds in baleen whales might be more common than is currently believed (Connor 2000). Studies based on identified juvenile individuals can help to understand whether these long-term bonds are initiated early in the whales' lives and maintained through adulthood.

Mother-calf pairs were the most frequent nearest neighbors to solitary juveniles of both sexes, a likely consequence of the high proportion of mother-calf pairs at the study site. However, this frequency was higher for juvenile females, who also initiated interactions more often and spent more time maintaining contact with mother-calf pairs than males. Cows initiated contact infrequently with juvenile females and never with juvenile males. Mothers appeared to be permissive toward juvenile females when juveniles approached their calves. Right whale female juveniles may learn maternal behavior by observing lactating females and by interacting with calves. Young females have the most to gain from practice parenting when first-born mortality and offspring investment by mothers are high (Whitehead and Mann 2000). Bottlenose dolphins and sperm whales appear to learn baby-sitting and other behavior from their mothers and other members of the adult population (Whitehead 1998, Connor *et al.* 2000, Rendell and Whitehead 2001). Future studies on kin relationships among the right whale females involved in these interactions should help us to understand learning of maternal behavior in this species.

Most social interactions during scans occurred among age peers. Females with offspring across species tend to be more solitary than other individuals (*e.g.*, chimpanzees, Goodall, 1986, Wrangham 1999; humpback whales, Clapham 1994; North Atlantic right whales, Hamilton 2002). In southern right whales, mother-calf pairs were the least social age class, adults were the most social, and juveniles were intermediate. This shows that juvenile right whales undergo behavioral and social changes during this transitional period of life. Social activities might be limited in their feeding grounds (Thomas and Taber, 1984) where juveniles may need to practice feeding techniques before they become efficient feeders (Hamilton 2002). Therefore, the time juvenile right whales spend with other whales at Península Valdés may be particularly critical for their normal social development.

Interspecific interactions

Kelp gulls are parasites on the skin and blubber of right whales in Valdés (Thomas 1988). Gulls directed most attacks to mother-calf pairs, who changed their behavior due to the attacks of gulls (Rowntree *et al.* 1998). Less than one in ten attacks were directed to juveniles. The rate of attacks per hour on juveniles was highest when they were in close proximity to mother-calf pairs, which mainly affected juvenile females. For instance, the social interactions of a juvenile female that approached five different mother-calf pairs over the course of 1 h, repeatedly ended after gull attacks. This implies that gull attacks have the potential to disrupt social interactions that could be relevant for the behavioral development of juvenile right whales in Valdés. Management measures to control the gull population for the reasons described by Rowntree *et al.* (1998) should be taken to reduce this impact.

The proximity of dusky dolphins and sea lions did not seem to affect the behavior of juvenile whales. Young sea lions have been observed swimming behind the turbulence generated by the tail of right whales (Payne 1995) and also dragging marine iguanas from their tails (Brown 1994) in what appears to be interspecific play.

Final remarks and conservation perspectives

Why should animals "waste time" being juveniles when they might be killed before they even try to breed? (Rowell 1993). Young right whales have a remarkable growth rate, growing between 28 and 35 mm per day for the first few months of life (Whitehead and Payne 1981, Best and Rüther 1992). The juvenile stage may provide the developing individuals time to grow to adult size, as well as to learn and practice effective complex behavior to gain social skills and to reduce ecological risks such as starvation and predation (Janson and van Schaik 1993, Rubenstein 1993). This is especially true in long-lived species like the right whale that begin to reproduce several years after birth. Young right whales may benefit from a reduction in orca predation risk by migrating to Península Valdés (Sironi *et al*. in prep.).

We have shown that juvenile right whale females spend a substantial time in the vicinity of and interacting with mothers and their calves as well as more time than males in body postures that are typical of adult females. Juvenile males engage in locomotory behavior patterns that resemble adult mating behavior with partners of similar developmental state. Testing the social learning hypotheses in right whales can be difficult without experimentation. However, our behavioral data show that the *opportunities* juveniles have at Península Valdés to learn and to practice skills when they engage in social activities are frequent and might be relevant for their future. Juveniles may also spend time at Valdés simply to become familiar with the environment where a significant amount of sexual and maternal behavior (and therefore, essential behavior for their reproductive success) will take place during their adult lives.

Juveniles are vulnerable animals (Sumich and Harvey 1986, Fairbanks 1993b, Rubenstein 1993, Payne 1995, Thompson 1998). During the present study, one yearling (Garra) got entangled in the mooring chains of a whale-watch boat; another juvenile cut the anchor rope of a research boat, and two juveniles had scars that were caused by propellers. Almost half of the known mortalities in North Atlantic right whales are due to anthropogenic causes (mainly ship strikes and entaglement) that affect juveniles more than other ages (Kraus 1990, 2002). There is a relatively low incidence of scars from boats, ships and ropes in the Península Valdés right whales (Rowntree *et al.* 2001). Effective long-term conservation policies should keep areas such as Golfo San José free of fishing gear and boat traffic to minimize anthropogenic mortalities and to secure natural habitats for the normal behavioral development of right whales.

Changes in behavior patterns may occur sooner in juveniles than in adults, and they occur much sooner than changes in reproductive outcomes or population size become evident (Snowdon 1990). Thus, detecting changes in the behavior of juveniles can serve as an early warning of environmental degradation. The present baseline description of right whale juvenile behavior in a relatively undisturbed site may prove important to assess the impact of human activities on this vulnerable species. Additionally, behavioral comparisons with other populations may prove valuable to protect right whales at other locations, particularly the closely related and highly endangered North Atlantic right whale.

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APPENDIX I:

OPERATIONAL DEFINITIONS OF BEHAVIOR PATTERNS FOR JUVENILE SOUTHERN RIGHT WHALES AT PENÍNSULA VALDÉS, ARGENTINA

The following behavior patterns were recorded during continuous focal animal samples in this study (see also Clark 1983, Thomas and Taber 1984, Payne 1986, Thomas 1986, Würsig *et al.* 1989, Würsig and Clark 1993, Rowntree *et al.* 1998).

Rest behavior:

Resting at the Surface (RS): a whale is horizontal at the water surface, motionless, with its back exposed to the air from the blowholes to the anterior area of the caudal peduncle, and no other whales are in close proximity (5 whale lenghts or less) interacting with it.

Resting Underwater (RUW): it is the same as RS but the whale is beneath the surface, with its back not exposed to the air, and the animal has to surface to breathe.

Social Rest (SR): same as RS and RUW, but the focal whale is 5 whale lengths or less from another resting individual.

Drifting (D): a whale is horizontal at the surface, with no body movements, but is being carried by previous swimming activity or by water currents.

Travel behavior:

Direction of travel is indicated with arrows (←→↑ ↓) and is relative to the shoreline.

Traveling Slowly at the Surface (TSS): a whale swims at the surface to change location, with its back exposed to the air, at a low speed (subjectively estimated).

Traveling Medium / Fast at the Surface (TMFS): the same as TSS but at a faster speed; "footprints" or surface swirls caused by the motion of the tail flukes are evident in the trailing path behind the swimming whale.

Traveling Slowly Underwater (TSUW): the same as in TSS but under the surface. The animal can be visually followed through the water or, if it swims too deep to be seen, it is observed every time it surfaces to breathe and its travel direction and speed are recorded.

Traveling Medium / Fast Underwater (TMFUW): the same as TSUW but at a faster speed.

Social Travel (SoTr): the whale travels as in the previous travel categories while one or more individuals also travel in the same direction at a distance of five whale-lengths or less from the focal individual.

Surface and aerial activity:

Surface Active (SA): a whale is active at the surface, causing evident white water with the movements of its body.

Active Underwater (AUW): the same as SA but right beneath the surface (with little or no white water), and at a depth that allows the whale to be seen by the observer. Occasionally, its flippers or flukes appear at the surface.

Rolling (Ro): a whale rolls at the surface along its longitudinal axis, so that its back, flanks and belly are sequentially exposed to the air.

Rocking (Rock): a whale repeatedly pushes its head up and down while at the surface and the body balances on a vertical plane.

Breaching (Br): a breach is a sudden jump of a whale out of the water, taking up to two thirds of its body out of it. A whale can breach once or repeatedly in a sequence of several breaches, and usually the one or two last breaches in a sequence are shorter than the previous ones.

Flipper Slapping (FlSl): slapping a pectoral fin against the water surface producing loud noises, while the whale lies at the surface on its side or belly up.

Lobtailing (Lt): slapping the dorsal or ventral side of the tail flukes against the water surface, producing a loud noise.

Tailing (Tl): a whale lifts its tail out of the water, and keeps it upright, motionless, at right angles to the wind ("sailing"); the whale is in an almost vertical position, head down, apparently keeping this posture by moving its pectoral fins.

Spyhop (Sh): a whale takes its head vertically out of the water, until the eyes are above the surface.

Belly Up (BU): a whale is upside down at the surface with its belly exposed to the air, with one or both pectoral fins out of the water or lying flat at the surface.

Social behavior and interactions:

Turning Toward (TuT): a whale swims on a straight line toward another whale or group of whales, actively decreasing the distance between them.

Turning Away (TuA): a whale swims away from another whale or group of whales, actively increasing the distance between them.

Active Pushing (AP): whale A pushes another whale B with its chin, on B's head, flanks or tailstock.

Passive Pushing (PP): whale A is pushed by another whale B with its chin, on A's head, flanks or tailstock.

Active Circling (AC): an individual swims around another whale or group of whales, five whale lengths or less from them.

Passive Circling (PC): an individual is encircled by another whale swimming five whale lengths or less from it.

Carrousel (Carr): ("milling") two or more whales swim in circles at the same spot, usually at one whale length or less from each other.

Active Rub (ARub): a whale strokes another whale using its flippers or tail flukes.

Passive Rub (PRub): a whale is stroked by the flippers or tail flukes of another whale.

Belly-to-Belly (BB): a whale A is at the resting position at the surface while another whale B positions itself belly up underneath A, head to head; the tips of the flukes of the belly-up whale B sometimes are visible at both sides of whale A. The genital slits of both whales are in potential or actual physical contact.

Inverted Belly-to-Belly (InBB): same as BB but head to tail.

Hug (Hug): same as BB but both whales are on one side at the water surface and crossing their flippers.

Other behavior patterns:

Gull Attack (GA): GA does not refer to a whale behavior pattern but to the habit of kelp gulls (*Larus dominicanus*) of actively feeding on the skin and blubber from the whales' backs. GA affect the behavior of right whales who usually arch their backs and swim away underwater after the attacks.

Galleon (Gal): a whale arches its spine to keep its head and tail up above the water surface and the middle of its back underwater. Usually performed after gull attacks (GA) and followed by travel at variable speeds.

Underwater (UW): a whale is submerged and out of sight and its behavior cannot be recorded for over 30 sec.

FIGURES

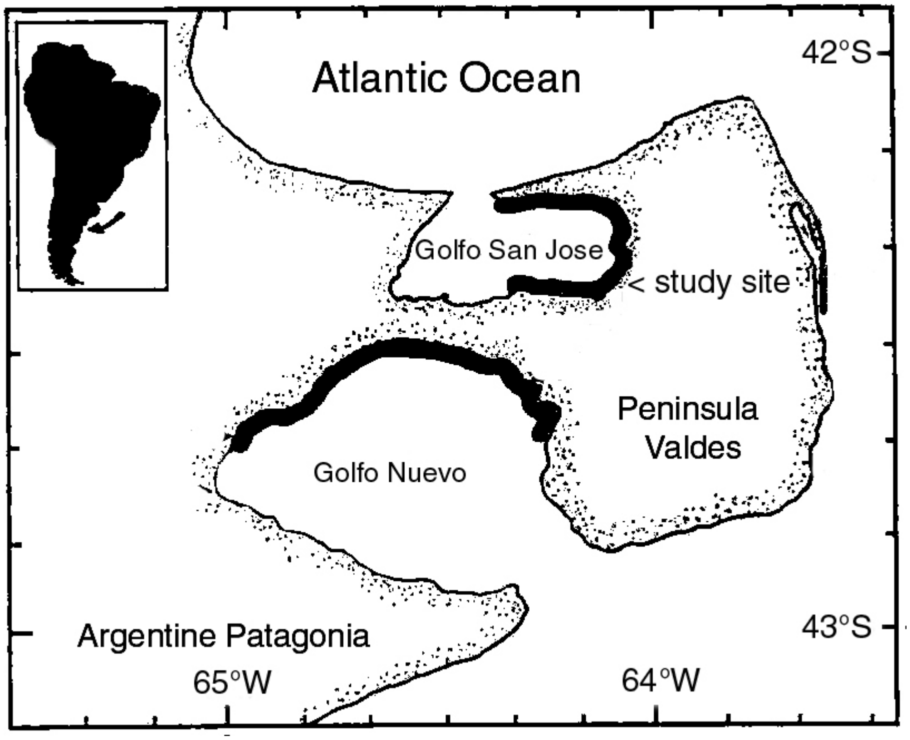


Figure 1. Map of Península Valdés showing the main right whale aggregation areas (shading) and the location of the study site (modified from Rowntree *et al.* 2001)

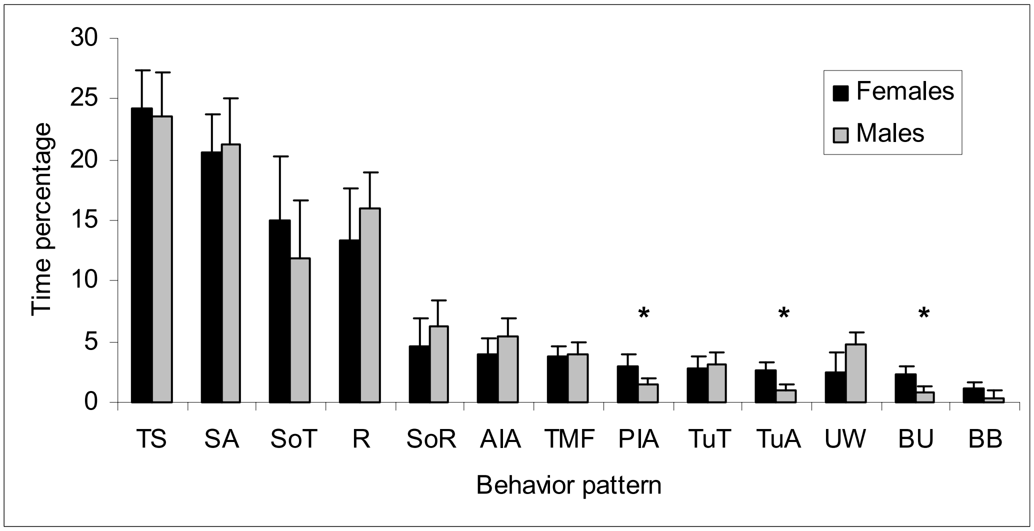


Figure 2. Time percentage (mean ± SE) juvenile females and males spent under the behavior patterns recorded during focal samples. TS: travel slow; SA: surface activity; SoT: social travel; R: rest; SoR: social rest; AIA: active interactions; TMF: travel medium / fast; PIA: passive interactions; TuT: turning toward; TuA: turning away; UW: underwater; BU: belly up; BB: belly-to-belly. Females spent significantly more time than males belly up (t = 3.13; df = 69; P = 0.003), as passive recipients during interactions (t = 2.3; df = 59; P = 0.024), and females turned away from secondary whales more frequently than did males (t = 2.59; df = 69; P = 0.012).

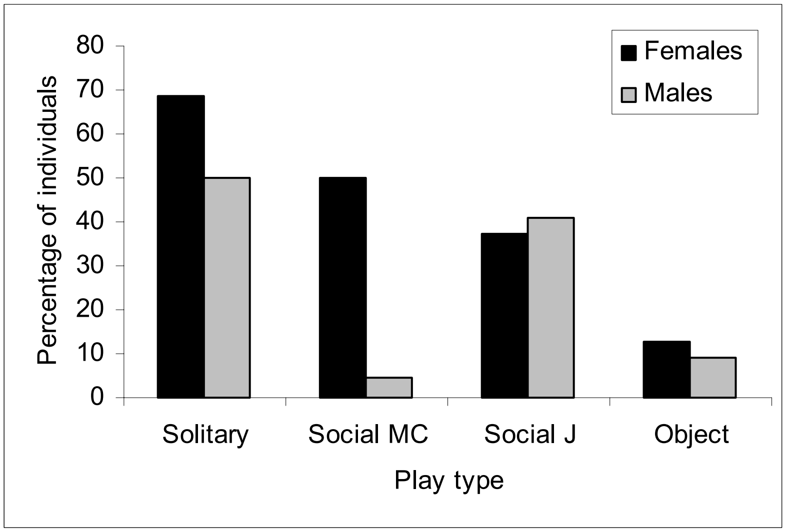


Figure 3. Percentage of juvenile females (N = 16) and males (N = 22) that were observed in solitary, social and object play. MC: mother-calf pair; J: juvenile.

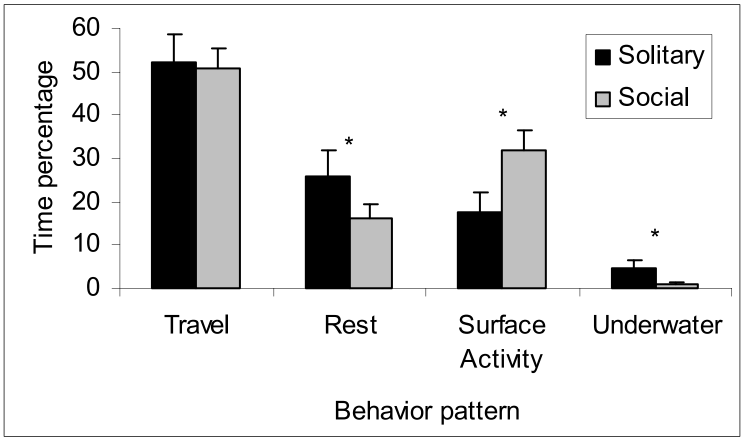


Figure 4. Overall behavior (mean time ± SE) in juveniles that were solitary (N = 28) or social (N = 49) during entire focal follows. Solitary juveniles spent significantly more time resting (t = 2.02; df = 75; P = 0.046) and underwater (t = 2.75; df = 75; P = 0.07) and less time in surface activity (t = -2.77; df = 75; P = 0.007) than social juveniles.

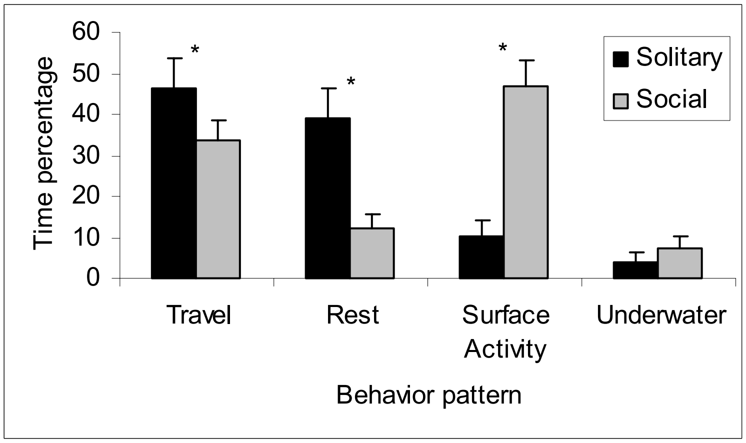
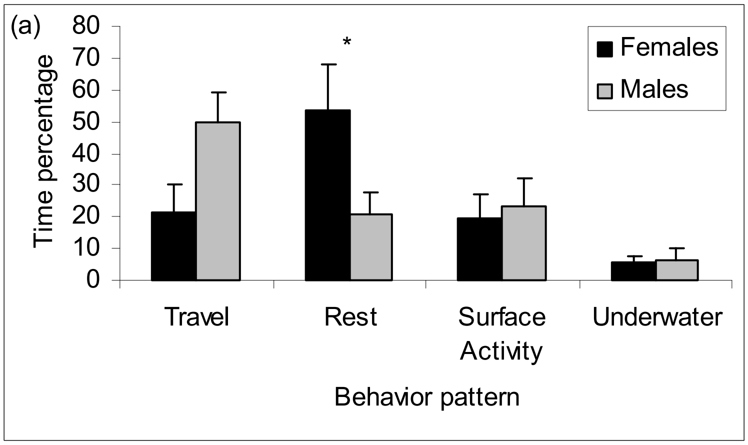
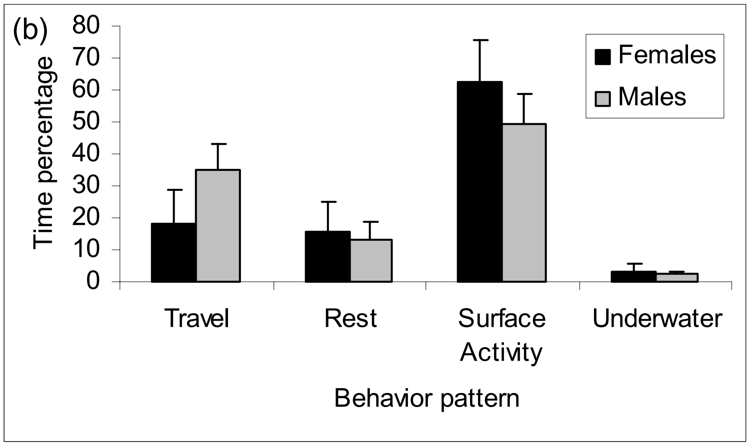


Figure 5. Overall behavior (mean time ± SE) in juveniles (N = 25) that were solitary and social at different times during the same focal follows. Juveniles spent significantly more time traveling (paired t = 3.74; df = 24; P = 0.001) and resting (paired t = 2.58; df = 24; P = 0.017) and less time in surface activities (paired t = -7.29; df = 24; P < 0.001) when they were solitary than when they were social.



(a) Solitary females (N = 7) and males (N = 11).



(b) Social females (N = 8) and males (N = 14).

Figure 6. Overall behavior (mean time ± SE) in (a) solitary and (b) social juvenile females and males. Solitary females spent significantly more time resting than solitary males ($t = 2.35$; $df = 16$; $P = 0.032$).

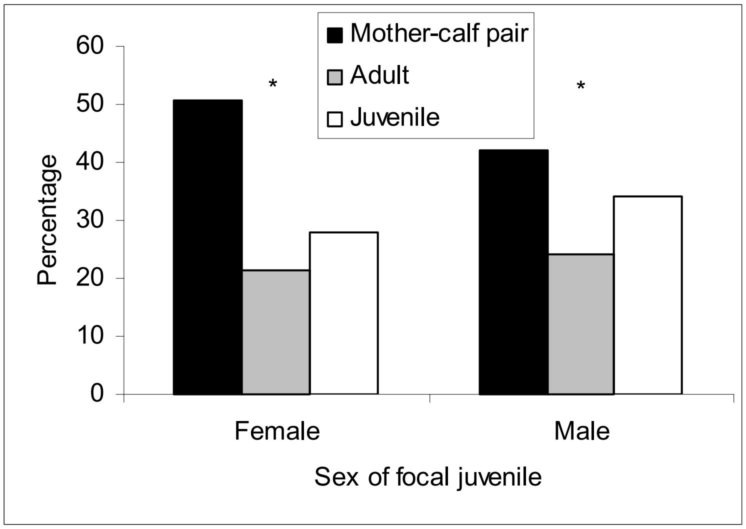


Figure 7. Percentage of nearest neighbors to solitary juvenile females (N = 61 nearest neighbors) and males (N = 50 nearest neighbors). The distributions for both sexes are significantly different from the expected based on the percentage of each age class at the study site (females: $\chi^2 = 6.46$, df = 2, P = 0.04; males: $\chi^2 = 13.61$, df = 2, P = 0.001).

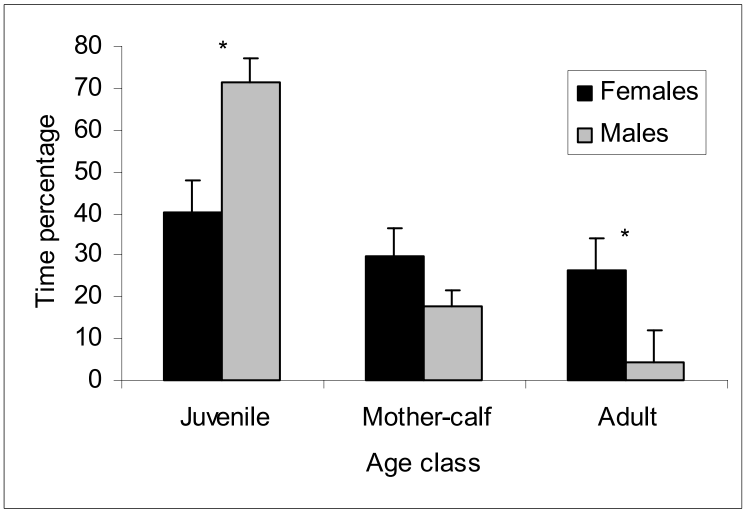


Figure 8. Time percentage (mean ± SE) juvenile females (N = 25) and males (N = 36) spent in social interactions with whales of all age classes. Juvenile females spent significantly less time with other juveniles (t = -2.13; df = 59; P = 0.037) and more time with adults (t = 2.27; df = 59; P = 0.027) than juvenile males.

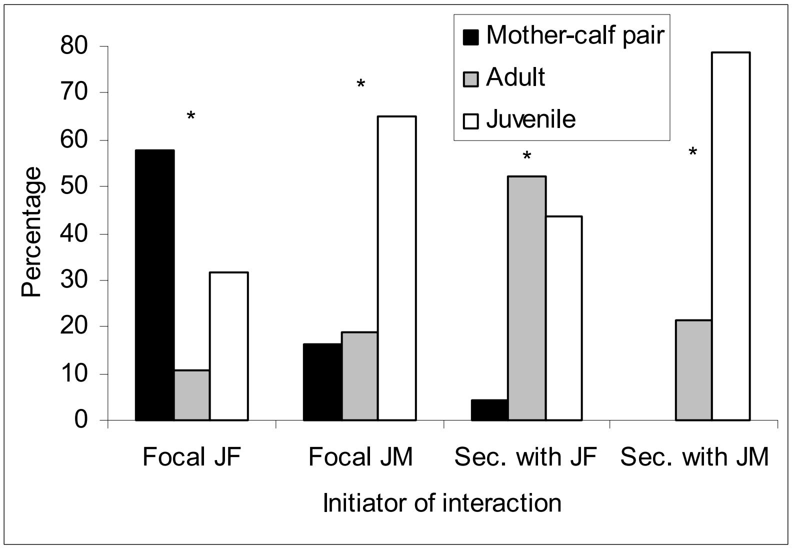


Figure 9. Percentage of interactions initiated by focal juvenile females (JF) and males (JM) with whales of all age classes, and by secondary whales (Sec.) of all age classes with focal juvenile females and males. The four distributions are significantly different from the expected based on the age class distribution of whales at the study site.

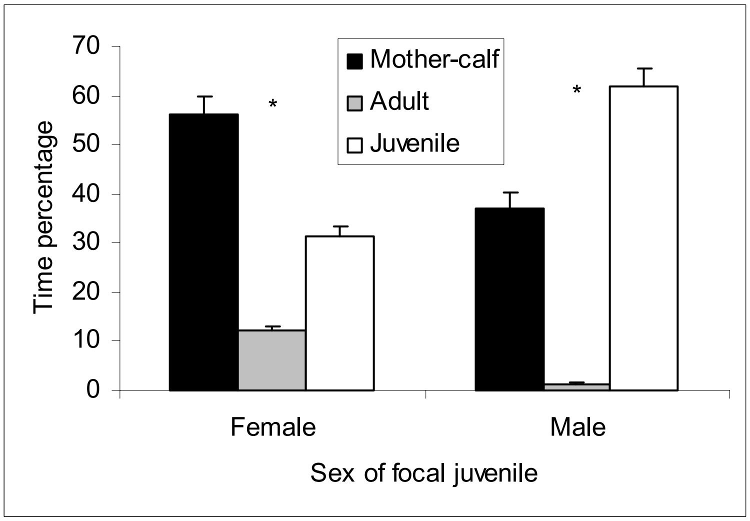


Figure 10. Time percentage (mean ± SE) juvenile females (N = 25) and males (N = 36) spent as actors with whales of all age classes. Juvenile females spent significantly more time as actors with mother-calf pairs (56.3 %) than with juveniles (31.3 %) or adults (12.3 %) (ANOVA, $F_{(2,72)} = 5.26$, $P = 0.007$). Juvenile males spent significanly more time as actors with other juveniles (61.7 %) than with mother-calf pairs (37.1 %) or adults (1.2 %) (ANOVA, $F_{(2,105)} = 7.5$, $P < 0.001$).

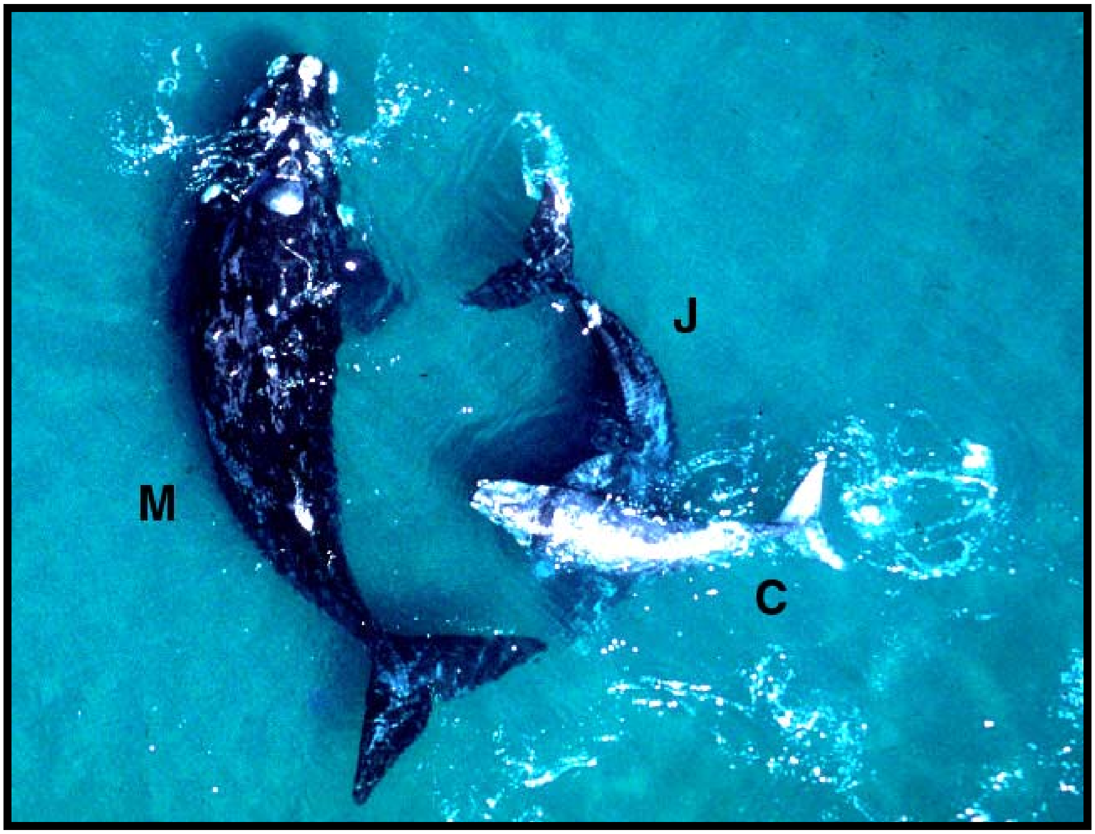


Figure 11. A juvenile right whale (J) interacting with the calf (C) in a mother-calf pair. M: mother.

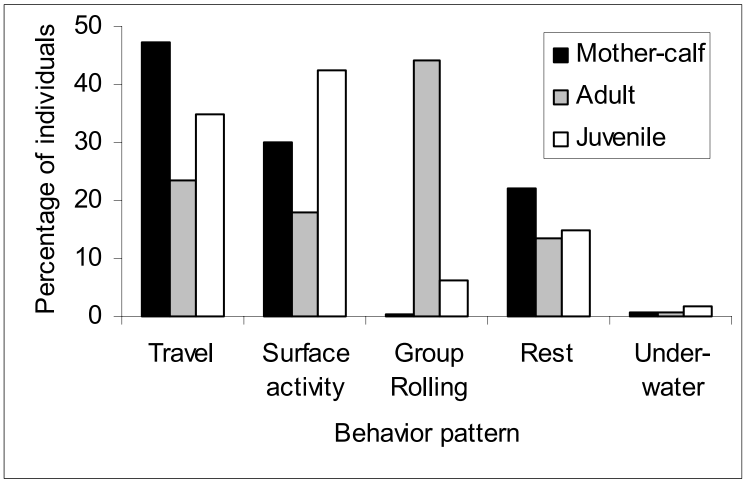


Figure 12. Percentage of individuals of each age class under the behavioral categories recorded during scans (N = 1,115 scans).

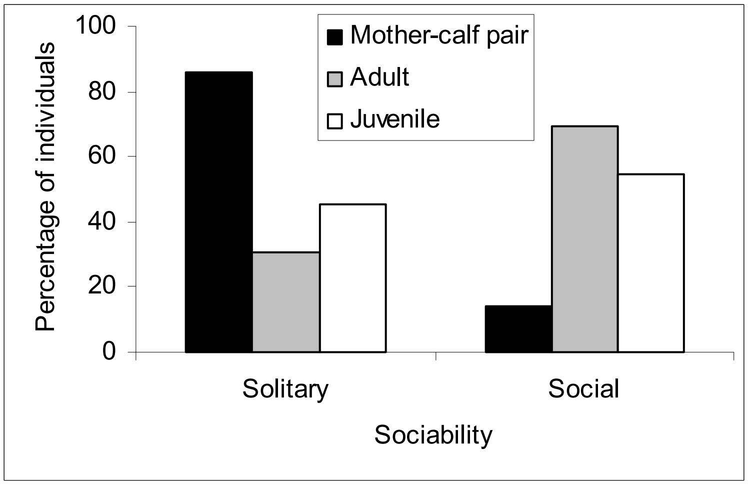


Figure 13. Percentage of solitary *vs.* social whales by age class during scans (N = 1,115 scans).

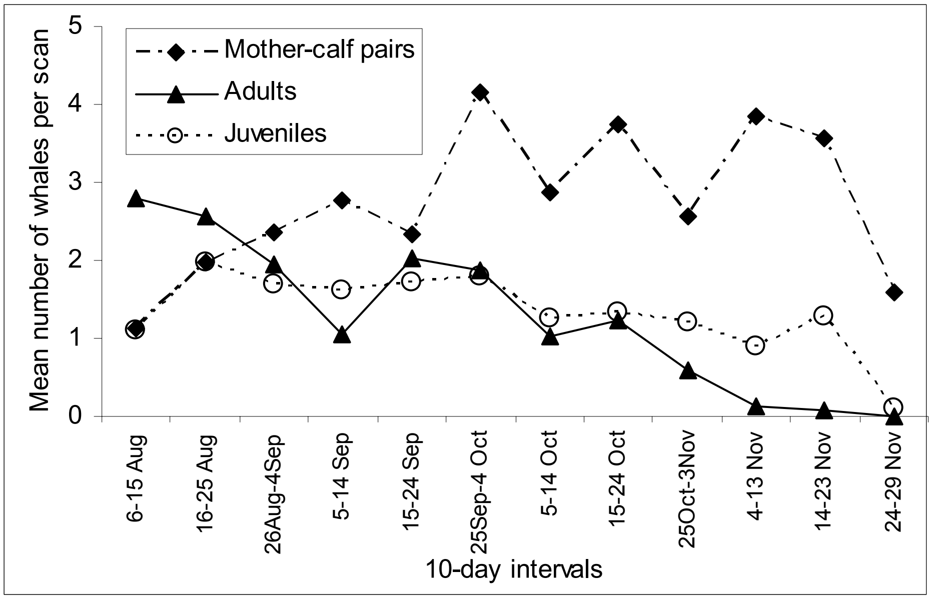


Figure 14. Mean number of whales per scan (N = 1,115 scans) per 10-day interval throughout the season.

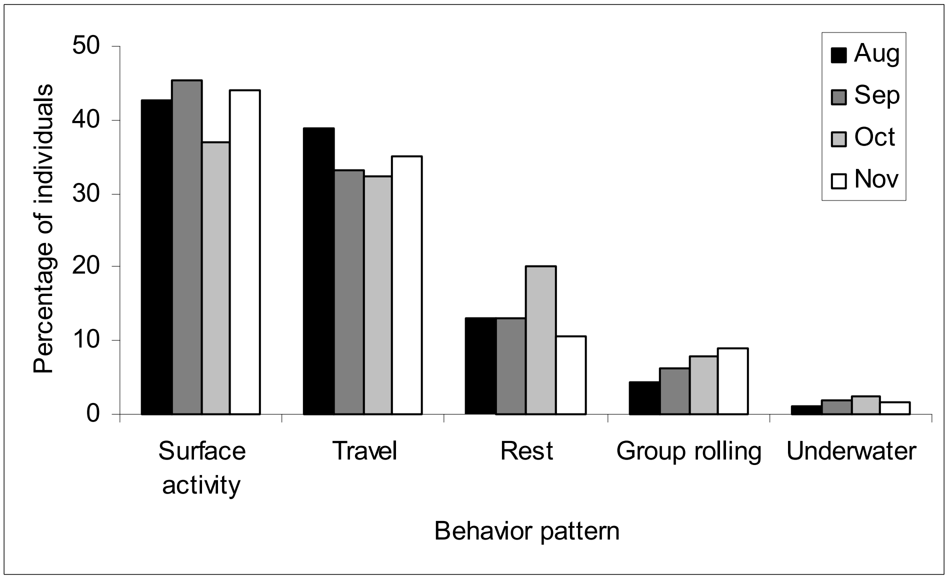


Figure 15. Percentage of juveniles under each behavioral category recorded during scans per month.

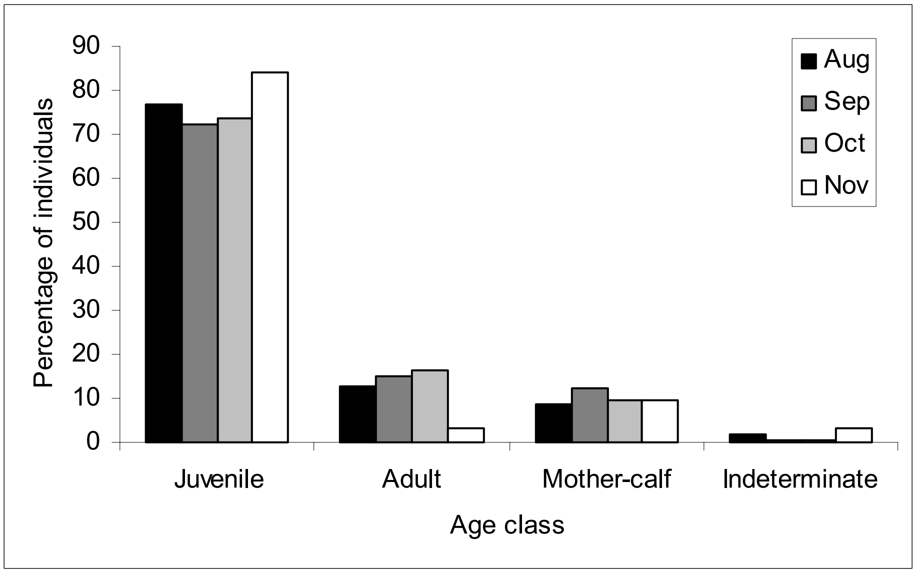


Figure 16. Percentage of juveniles interacting with whales of each age class during scans per month.

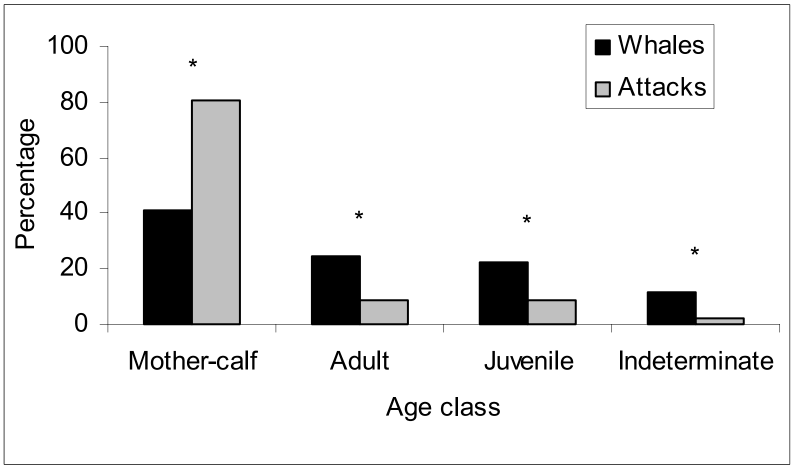


Figure 17. Whale age distribution and distribution of gull attacks per whale age class during scans. The distribution of gull attacks among all whales was significantly different from the age class distribution of whales at the study site ($\chi^2 = 426.2$, df = 3 , $P < 0.001$).

CHAPTER 4

AGE ESTIMATION OF NORTH ATLANTIC RIGHT WHALES (*Eubalaena glacialis*) BY ALLOMETRIC MEASUREMENTS ON PHOTOGRAPHS

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ABSTRACT

Models to predict the age of North Atlantic right whales (*Eubalaena glacialis*) were developed using shipboard lateral photographs of their heads. Models based on allometric ratios of head measurements explained three quarters or more of the variability in the square root of age as response variable. Model fit was lower for whales with continuous callosity patterns. Changes in the curvature of the rostrum and the height of the dome are the best predictors of age in the external anatomy of the head of right whales. The accuracy of age prediction decreased with age: it was maximum for calves and minimum for whales older than 8 yr. Mean coefficients of variation of repeated measurements ranged from 0.31 to 4.11 %. Photographs taken at medium distance from the whales (photographs where the head length is equal or greater than one half of the frame width) are better than those taken close or far, in order to avoid biases related to the angle of view of the subjects and to the small size of the measurements, respectively. This photogrammetric technique is non-intrusive, simple and inexpensive. Because it is based on ratios of measurements, it eliminates the need to know the distance to the subjects or to have a scale object close to them to estimate the age of live right whales.

INTRODUCTION

Knowing the age of individuals in the wild is critical for understanding population dynamics and for estimating the demographic parameters of a species. Depleted whale stocks must be monitored by means of benign techniques that do not rely on disturbing or killing the whales to determine life history parameters and population trends (Whitehead and Payne 1981, Kraus *et al.* 1986, Best and Rüther 1992, Spitz *et al.* 2000).

In this context, several non-invasive techniques have been used to measure the size and thus estimate the age of cetaceans. Some rely on a scaling object of known size that is photographed from an aircraft in the same frame as the whale that is being measured (Whitehead and Payne 1981). Others combine altimeter readings and the focal length of the camera lens to estimate the size of whales from aerial photographs (Cubbage and Calambokidis 1987, Best and Rüther 1992, Ratnaswamy and Winn 1993, Angliss *et al.* 1995, Perryman and Lynn 2002). Photographs taken from boats also allow estimation of body sizes of sperm whales (Gordon 1990, Dawson *et al.* 1995). Underwater videogrammetry has been used to measure humpback whales while gathering data on individual identification and behavior (Spitz *et al.* 2000).

Right whales (*Eubalaena*) can be identified individually by the unique pattern of callosities on their heads (Payne *et al.* 1983, Kraus *et al.* 1986). Long-term studies have produced photoidentification catalogs of southern right whales (*E. australis*) in the SW Atlantic (Payne and Rowntree 1984) and North Atlantic right whales (*E. glacialis*) in the NW Atlantic (Hamilton and Martin 1999). Photographs are taken from a variety of platforms, including boats and airplanes. The small size of the callosity pattern of newborn calves and the large patches of cyamids on their heads (Rowntree 1996) make the identification of calves difficult. As a consequence, whales that were not identified in their year of birth and that are resighted in later years are of unknown age.

The head of right whales shows positive allometric growth from their calf year to adulthood, although the relationship is not sufficiently strong to estimate growth during the first year of life (Whitehead and Payne 1981, Best and Rüther 1992). The overall shape of the head changes with age; in profile the head appears "truncated" and with a raised coaming in calves (Hamilton and Martin 1999). The rostrum flattens as the animals grow. These head shape changes, if properly quantified, could provide a basis for age estimation.

We developed a technique to estimate the age of N Atlantic right whales based on a combination of ratios of allometric measurements of their head taken from lateral shipboard photographs of whales of known ages. The main aim of the technique is to predict the age of whales whose year of birth is unknown using allometric ratios. The application of this method could allow better estimations of population parameters that are based on the age of individuals. The technique could be applied to all right whale populations and could improve the assessment of the demographic parameters of right whales throughout the northern and southern hemispheres.

MATERIALS AND METHODS

Photographs used. Measurements were taken on 374 photographs of 62 whales (30 females and 32 males) born between 1986 and 1996. The year of birth was known for all the whales selected. The photographs are stored in the catalog compiled at the New England Aquarium in Boston (for a catalog description, see Hamilton and Martin 1999). The photographs used were shipboard color slides that showed lateral views of the rostrum, the upper portion of the lower lip, and the back of the whales above the water surface. Photographs of some whales were not available for some years due to individual differences in sighting and photographic records. A description of photoidentification problems of N Atlantic right whales can be found in Kraus *et al*. (1986).

Measurements taken. Fig. 1 shows the measurements taken on the photographs. In order to make this technique simple to use and available to most right whale researchers, all measurements were made directly on the projected image of slides on a white paper screen to a precision of 0.5mm. The distance between the lens of the projector and the screen was 180cm, and the size of the projected image was 40 x 60cm. Sketches of the head profile (including the outline of the callosities and the lower lip) of some whales were made by projecting the image on a sheet of paper and by drawing on the paper along the profile. The sketches of each individual were visualized simultaneously to compare the changes in the head profile at different ages.

The callosity nomenclature used here follows that proposed by Payne *et al.* (1983). Some terms used in this paper are defined in Table 1. In other studies (*e.g.*, Whitehead and Payne 1981, Best and Rüther 1992, Ratnaswamy and Winn 1993), the rostral length was measured from the tip of the snout to the center of the blowholes. Here, the rostral length was measured from the front tip of the bonnet (visible in more lateral photographs than the tip of the snout, which is frequently underwater) to the rear tip of the coaming (which in lateral photographs can be located with a smaller margin of error than the center of the blowholes). The height of the dome (the raised portion of the rostrum where the coaming sits) was measured from the highest point of the coaming to the imaginary line that connects the isthmus to the lower margin of the post-blowhole island. The remaining measurements are self-explanatory from Fig. 1.

Photograph quality. Two variables in the photographs (angle and endpoints) were considered to grade the quality of the photographs for the measurements, with 1 indicating highest quality and 4 indicating lowest quality. The position of the whales on the photographs (or “angle”) was graded as 1 (whale perpendicular to the line connecting it to the photographer and horizontal at the surface, producing a full lateral view of the emerged portion of the head), 2 (slight angle: whale in slight diagonal to the photographer, *e.g.*, approaching or leaving, but flat relative to the surface), 3 (same as 2 with a marked angle) or 4 (same as 2 or 3, but whale not horizontal). In photographs graded as 4, the whale was tilted along its longitudinal axis, or the photograph was taken from a high perspective, *i.e.*, the whale was very close to the photographer standing relatively high on a boat, and the whale was viewed from above.

The endpoints of the dimensions measured on the whales' head were graded as 1 (both endpoints visible and clear), 2 (both endpoints visible but slightly blurred), 3 (one endpoint not visible but visual extrapolation was possible) or 4 (both endpoints not visible and extrapolation was necessary for both). Especially important for measuring rostrum length were the front tip of the bonnet (underwater in some photographs) and the rear tip of the coaming.

Not all measurements were affected equally by the variations in the quality of the angle and the endpoints. For example, a marked tilt along the longitudinal axis of a whale significantly affected vertical measurements (*e.g.*, valley-zenith) but did not affect longitudinal measurements (*e.g.*, rostral length) if the whale was perpendicular to the photographer. As a result, the same photograph could be graded as 1 for a variable affecting some measurements and as 4 for a variable affecting others. Measurements taken on photographs graded 1 and 2 were classified as "high quality" (HQ) and those graded 3 and 4 were classified as "low quality" (LQ). The photographs with LQ measurements were subdivided into three groups: group 1 (those with grade 3 or 4 for angle), group 2 (grade 3 or 4 for endpoints) and group 3 (grade 3 or 4 for both angle and endpoints) (see Table 2 for sample sizes). HQ and LQ photographs were analyzed separately.

A subset of photographs of whales with continuous callosity pattern was analyzed separately in order to determine how the particular features of this type of pattern may affect age prediction using the present technique.

The distance between the photographers and the whales was unknown. However, the relative size of the head of the whales on the projected image was used as an indication of distance. Photographs were graded as 1 (or "close") when the rostral length represented at least one half of the length of the image (30 cm or more on a 40 x 60 cm projected image), 2 ("medium", rostral length between 10 and 29.9 cm) or 3 ("far", rostral length less than 9.9 cm). These three "distance categories" were used to compare the whale-to-photographer distance distributions between HQ and LQ photographs. This was done to evaluate a possible distance effect in the age predicting capability of the models. The age distribution of whales was also compared between the two samples.

The photographs in the catalog were contributed by 24 organizations and 55 individuals (Hamilton and Martin 1999) and were taken over many years with different cameras and lenses from a variety of platforms and in different formats (Kraus *et al.* 1986). For this reason, the sources of error at the moment of photographing the whales varied, and an estimation of this error was practically unfeasible.

Ratios and data analysis. In this paper, the terms "estimate" and "predict" will be used interchangeably. In the statistical terminology, the word "prediction" involves an inherent uncertainty that is ascribed to each individual whale, as opposed to an average over all whales whose age is "estimated" using the same explanatory variables. The application envisioned here is to estimate / predict the age of whales on the date they were photographed.

Using allometric ratios to estimate the age of whales is particularly convenient because ratios are independent of the distance to (or altitude above) the whales at the moment of photographing them, and because they do not need to rely on a scale or object of known size. The measurements taken on the photographs (Fig. 1) were combined to produce 33 ratios to describe the allometric changes in the head of right whales. Of these ratios, three involved the lip apex; four were designed to measure changes in rostral length; four measured changes in the coaming; 11 combined the length of the rostral islands with rostral length, and 11 were combinations of the measurements involving the curvature of the rostral profile (those involving the zenith).

A study of intra- and interobserver errors was conducted to evaluate the precision of the measurements taken. Measurements of rostral length, coaming length, island length, coming-to-zenith, valley-to-zenith and lip apex-to-isthmus (Fig. 1) were taken 10 times on HQ photographs from each of nine individual whales of different ages by four readers. The coefficients of variation (CV) for the measurements taken by each reader on each trait were calculated to quantify the intraobserver errors. A two-way non-parametric ANOVA was computed using the mean, standard deviation (SD) and CV, respectively, from the 10 repeated measurements for each reader on each trait of each whale. The two factors were reader and whale. A separate analysis was conducted for each of the six traits.

Multiple regression analysis was performed with all photographs and separately within the HQ and the LQ subsamples using the REG Procedure of SAS version 8.2

(SAS Institute Inc. 2001). Early in the analysis it was found that using the square root of age as the response variable (instead of age) led to homogeneous variances as required by standard regression. Exploratory regressions were used to fit linear relationships between the square root of age as dependent variable and the 33 ratios as independent variables. Subsets of the best predictors (based on their higher frequency of occurrence in the models with the largest R^2 in the exploratory analysis) were used in further analyses. The REG procedure requires that all independent variables in each observation have a value for the observation to be included in the analysis. Because some measurements were not possible in some photographs, the ratios involving those measurements could not be calculated and therefore, those photographs were excluded from the analyses by the procedure. As a consequence, sample sizes for each group of photographs vary.

To determine if there were sex differences in age prediction, we plotted the true age *versus* predicted age of females and males and calculated the corresponding residuals. The means of the residuals for each sex were compared in the HQ photographs. Using the prediction model for the HQ photographs, we added an indicator variable for gender to explore whether gender increased the prediction capability of the model.

To validate the model for the HQ photographs, we divided the photographs into four independent quarters. We used three quarters of the photographs to fit the model and predicted the age of the whales in the remaining quarter of the photographs. We repeated this process four times (one for each quarter withdrawn). We ran a Separate Slopes Analysis (ANCOVA) to test for differences in the relationship between true and predicted age among the four quarters.

To provide an estimate of age prediction error, we obtained the mean and SD for each of the four predictor variables in the HQ sample model. Using all possible combinations of the three values (mean, mean + 1 SD, mean - 1 SD) for the four variables, we fit the model to obtain predicted values of the square root of age with the corresponding 95% confidence intervals (CI) for the predicted values. The values of square root of age were then transformed into true values of age to calculate the CI.

Chi square and Fisher's Exact tests were used to compare the age distribution of whales and the distance distribution in the HQ and LQ photographs. Tests were two-tailed and the level of significance was set at $\alpha = 0.05$.

RESULTS

An average of 6.02 slides (SD = 2.69, range = 2-13) of each of the 30 females and 32 males at different ages were used. The age of whales spanned from 0 (calf year) to 14 yr, with a mean age range of 8.34 yr (SD = 2.71). The procedure selected 123 HQ slides, 83 LQ slides (50 in group 1, 18 in group 2 and 15 in group 3), and 22 slides of whales with continuous callosity pattern to fit the models.

High quality (HQ) photographs

Using the REG procedure of SAS (SAS Institute Inc. 2001) with the HQ photographs, the mean squared error (MSE) was minimized (or equivalently, the adjusted R^2 was maximized) using a model with four predictor variables involving only six measurements (*i.e.*, adding more variables led to an increase in the MSE). Rostral curvature and dome height showed the greatest variation with age and thus, were the best age predictors. The six measurements were dome height, coaming length, rostral length and the three measurements involving the zenith. The best four predictor variables (Table 2) were *DH/CL, (DH+VZ)/RL, BZ/VZ* and *CZ/VZ*. All had partial p-values <0.001 except for *CZ/VZ*. However, we included all four variables in our final model since we used minimum MSE as our criterion for subset selection. The algebraic sign indicates the effect of an increase in the value of the predictor variable on the predicted square root of age. Thus, an increase in *(DH+VZ)/RL* results in a decrease in square root of age. Caution should be excercised in interpreting the coefficient estimates due to correlation among the four predictor variables (multicolinearity).

The R^2 value of 0.747 was quite high suggesting that about three quarters of the variability in the square root of age was explained by the four predictor variables. The equation can be used as a basis for age prediction in right whales. Thus, with the values for the four allometric ratios obtained from a photograph, the predicted square root of age of the whale photographed, $\hat{Y}_P$, is obtained as

$$\hat{Y}_P = 2.201 + 1.125\, DH/CL - 22.841\, (DH+VZ)/RL + 1.396\, BZ/VZ + 0.821\, CZ/VZ$$

Using standard regression techniques, a 95% confidence interval for $\hat{Y}_P$ led to a half width of approximately 1.12. Thus, one can be 95% “confident” that the true square root of age of a whale falls within ±1.12 of the value predicted by the model. However, when the response variable (square root of age) is transformed to age, the width of the CI increases with the predicted age of whales. Some representative approximate 95% CI for some predicted values of age are (lower bound < predicted age < upper bound)

0* < 0.1 < 1.49

0* < 1 < 4.49

0.21 < 2.5 < 7.3

0.77 < 4 < 9.73

2.33 < 7 < 14.18

3.53 < 9 < 16.97

(*constrained to 0 on biological grounds)

The Separate Slopes Analysis indicated that there were no significant differences in the relationship between true and predicted age among the four quarters of the photographs used to validate the model. When the age of the whales in each quarter was estimated using the model fitted with the remaining three quarters, the resulting four slopes of the true *versus* predicted age were close to 1 (range = 0.91 – 1.12) and were not significantly different from each other (ANCOVA, *F* = 0.88, df = 3, *P* = 0.45).

A comparison was conducted between the true age of whales and the predicted age based on our model to determine if there were any systematic problems in our prediction equation. Overall the model fit well. There was less variability and higher accuracy in age prediction among calves and juveniles than among older whales (Fig. 2). For the whales available in our data set, there was a slight tendency for the predicted age to be smaller than the true age for older whales. This is most apparent in Fig. 3, where the "true" number of individuals is larger than the predicted in the three oldest age categories. More data points in these age categories will be needed to reduce this bias.

The mean residuals obtained from the plot for HQ photographs in Fig. 2 were not significantly different for females and males (one-way ANOVA, *F* = 2.07, df = 1, *P* =

0.15). When we added an indicator variable for gender in the HQ model, the improvement in the R^2 was negligible (from 0.747 to 0.749). The partial P value of this variable in the model was non-significant ($P = 0.33$). These results indicate that there are no apparent sex differences in the anatomical traits of the head of right whales that were used for age prediction.

Low quality (LQ) photographs

The same procedure was followed for the three groups of LQ photographs. Using the minimum MSE criterion, five predictor variables were selected for groups 1 and 3 and two variables for group 2. The models are shown in Table 2. All variables had significant partial p-values except for the intercept in group 1. The R^2 values in the three models (0.795, 0.747 and 0.890) were high. However, it should be noted that the sample sizes were relatively low, especially in groups 2 and 3. Therefore, the predicting capability of models based on LQ photographs of these two groups should be taken with caution.

When all 83 LQ photographs were used to fit one model with five variables, the resulting R^2 value (0.71) was lower than the individual R^2 values obtained in each of the models that discriminate among the three types of LQ photographs. Similarly, when the four-variable model developed for the HQ photographs was used to predict the age of whales in the three groups of LQ photographs, the R^2 values also decreased (0.68, 0.50 and 0.78 for groups 1, 2 and 3, respectively), suggesting the need for different models with different quality photographs.

As with the HQ photographs, age prediction with LQ photographs was more accurate for young whales (Fig. 2). The models also underestimated the age of older whales in the LQ sample (Fig. 3).

Whales with continuous callosity pattern

We attempted to develop an age prediction model specific for individuals with continuous callosity pattern. However, some measurements could not be taken on photographs of these whales due to the peculiar anatomical characteristics of this type of pattern. Thus, the number of slides used by the procedure to fit the model was quite low (22). Our chosen model, with four predictor variables, had lower R^2 (0.628) and higher MSE compared to the HQ and LQ photograph models, and the partial p-values of the variables were also higher (Table 2). It is interesting to note that this was the only model that incorporated a ratio with the isthmus-apex measurement.

Age and distance distributions

In order to test for a possible relationship between whale age and photograph quality, we compared the age distribution of whales in the HQ and LQ samples. We divided the age of whales into seven categories: 0, 1, 2, 3, 4-5, 6-8 and 9 yr of age or older. We found no significant differences in the age distribution of whales in the two samples (HQ $x = 3.78$ yr, SD = 3.34; LQ $x = 3.74$ yr, SD = 3.46; $\chi^2 = 3.002$, df = 6, $P = 0.81$).

Similarly, we compared the whale-to-photographer distance distribution in both samples to test for a possible distance effect. In this case, we compared the three distance categories (1 = close, 2 = medium, 3 = far, as defined above) among the HQ photographs and the three groups of LQ photographs. We found no significant differences in distance distribution among the samples (mode = 2 in all samples; Fisher's Exact Test, df = 6, P = 0.62). The majority of photographs in both samples (78.9% of HQ and 82.8% of LQ photographs) were taken at medium distance, but a slightly larger percentage of photographs in the LQ sample (12.9%) were taken at longer distance than in the HQ sample (9.7%).

To analyze the prediction capability of the model for close and far photographs, we divided the HQ sample into two groups of similar size based on distance, using the median of the rostral length to separate close (= 1) *versus* far (= 2) photographs. We fit the original four-variable model developed with the HQ photographs to each of the two groups. There was virtually no difference in the performance of the model between the two groups (group 1 = close, $R^2 = 0.789$, group 2 = far, $R^2 = 0.798$).

Estimation of measurement precision and reader error

Coefficients of variation (CV) were obtained from 10 repeated measurements of six traits taken by four readers on nine different whales. The CVs for the traits ranged from 0.31 to 4.11% (Table 3). The CVs were lowest for the longest traits (*e.g.*, coaming and rostral lengths) and highest for the shortest traits (*e.g.*, coaming-zenith and valley-zenith distances) among all readers. The measurements of the coaming-to-zenith distance showed the highest variation, with CVs ranging from 0 to 10.9% in one reader.

There were no significant differences among readers in the mean values obtained for measurements for four of the six traits (Table 3). The mean of the coaming-to-zenith distance showed differences among observers, likely due to the small values of this trait (x = 3.96 mm). Although the mean rostral length also showed statistical differences among readers (likely due to the small CV), the absolute magnitude of this difference is minimal (mean values of rostral length for the nine whales measured by the four readers were 137.92, 138.01, 138.09 and 138.24mm).

Not surprisingly, there was a highly significant whale effect in the mean values of the six traits measured (Table 3), indicating the anatomical variability among whales as well as differences in whale-to-photographer distance in the photographs used for the precision estimation test.

DISCUSSION

Age prediction, ratios and models

The models allow for age estimation of North Atlantic right whales by allometric measurements of their heads taken from shipboard lateral photographs. The technique is easy to apply and inexpensive, as it does not require sophisticated and costly equipment to take the photographs and measurements. Because ratios are used, the method does not rely on objects of known size on the same frame of the whales photographed (Whitehead and Payne 1981) or on the distance (or altitude) from the camera to the animals (Best and Rüther 1992, Angliss *et al.* 1995, Perryman and Lynn 2002) to obtain the values for the age predictor variables. Like other techniques developed since the 1970's, this method is non-invasive and does not require disturbing or killing of whales to obtain vital information such as age-related population parameters.

A total of 10 measurements were taken on the whales' heads (Fig. 1). However, the HQ and the LQ group 1 models used only six measurements, and the remaining models used only five. Once the quality of a photograph is determined, a reader needs only to take the necessary measurements for the specific model to predict the age of the whale on that photograph, which simplifies the use of the technique.

The models work particularly well with younger individuals, while age prediction for whales older than 8 yr has wider confidence intervals. The models underestimate the age of older whales. Very few whales were predicted to be 10 yr old or older, and none was predicted to be 12 or more (see Fig. 3). Although no significant differences in age distribution between the samples were found, the overall data set was skewed to younger whales and does not represent the age of the entire population evenly. Adding more photographs of older whales could possibly improve prediction at older ages. However, the flattening of the rostrum as the whales grow older (as shown in Fig. 1), with the resulting loss of age-related anatomical changes in this trait, may hinder age prediction for older whales. The mean age at first parturition is estimated at 11 yr for this population (Kraus 2002). Thus, the method would work best for young whales, allowing for more accurate age prediction of individuals who have not yet reached puberty.

Best and Rüther (1992) suggested that systematic technical biases in aerial photographs of right whales tended to underestimate the size (and therefore the age) of whales. Whitehead and Payne (1981) obtained greater confidence limits for the mean growth curve of southern right whales at older than at younger ages. The marked curvature of the rostrum or, similarly, the notable height of the dome, in calves and young animals (Hamilton and Martin 1999) appears to be the best anatomical indication of youth in the head of right whales. This is suggested by the fact that rostral curvature (as indicated by ratios including the zenith measurements) and dome height consistently appeared as predictor variables in all of the models, with the exception of the dome height in the continuous callosity pattern model.

The majority of photographs used were taken in the summer (Jul-Sep), when most calves of the year were between 7 and 9 mo old. If more lateral photographs of the same whales were taken throughout their first few months of life (when changes in the rostral curvature are more prominent), they could be used to develop a more accurate age prediction model for young right whales. Also, in our sample, all whales that were younger than 1 yr were classified as being ‘0 yr old.’ The models predicted these whales to be between 0.25 and 0.37 yr old on average, which is closer than zero to their true age at the time of being photographed. Others have attempted to describe growth in right whale calves by using the ratio of rostral length to body length, but they found no significant positive allometry in this ratio during the first year of life (Whitehead and Payne 1981, Best and Rüther 1992). Given that the aim of the present study is to estimate the age of whales to the nearest year, we think that our technique is appropriate for assigning a whale to the calf year when other indications (*e.g.*, its repeated association with an adult female, or time of the year) are not available (*cf.* Clapham *et al.* 1999).

The rostral length expressed as a percentage of total body length has been used to predict age in southern right whales older than 1 yr (Whitehead and Payne 1981, Best and Rüther 1992). Rostral length appeared in all of our models, demonstrating its importance to predict age when combined with other dimensions of the whales' heads. Contrary to the HQ and LQ models, where rostral length appeared in combination with the rostral curvature and the dome height, the rostral length appeared in combination with the isthmus-to-apex distance in the model for whales with continuous callosity pattern.

The model for whales with continuous callosity pattern was the only one to include the isthmus-to-apex distance, and was the only model where the dome height was absent from all ratios. The continuous callosity tissue along the midline of the rostrum of these whales may increase the relative height of the isthmus and distort the typical curvature of the rostrum from a lateral view. One result of this is an increase in the isthmus-to-apex distance compared to whales with discontinous callosity pattern, for which this measurement was not a predictor of age. The increase in the isthmus' height may decrease the measurement of the dome height, potentially removing the positive allometry with age that dome height showed in whales with discontinuous callosity patterns. Also, because the bonnet and the coaming are one indistinct callosity with no discrete endpoints separating them, the location of the margins of 'bonnet' and 'coaming' to take the zenith measurements in whales with continuous pattern is approximate and should be taken with caution. Difficulties with the photo-identification of whales with continuous patterns have been described by Kraus *et al.* (1986). It is important to note that the sample size used to fit the model for whales with continuous callosity pattern was quite small, and these effects could disappear with a larger sample.

Right whale callosities enlarge as the head grows (Payne *et al.* 1983). Islands may be rounder in calves than in adult whales and may elongate as the rostrum grows. Thus, elongated islands could be an indication of older age. No ratios of the island length to rostral length appeared in the models. The width of the islands cannot be measured on lateral photographs. If dorsal (aerial) photographs were used, a ratio of island length to island width as an indication of the islands' 'shape' could be calculated. This shape could potentially show positive allometry with age (longer in older whales) and be used as an age predictor. Also, the absence of island ratios in the models presented here may be due to the lack of rostral islands in whales with continuous callosity pattern (Kraus *et al.* 1986), and to some whales having few islands that may be on the opposite side of the head as viewed on the photograph used for a particular year. As a result, these photographs had no values for the island ratios and were excluded by the regression procedure for model fitting.

With the exception of the model for whales with continuous callosity pattern, all models had R^2 values higher than 0.74. When the HQ model was applied to LQ photographs, the resulting R^2 decreased, suggesting that different models should be used with photographs of different qualities. Although the forms of the allometric ratios varied among models, a few traits (most notably, rostral curvature and dome height) appeared to be the most consistent age predictors among models. Similarly, when the appropriate allometric relationships are chosen, total length (and therefore, age class prediction) in fin whales can be reliably estimated when direct measurements are not possible

(Ratnaswamy and Winn 1993). While the selection of predictor variables based on maximum R^2 and minimum MSE can be statistically suitable, no model can be positively identified as the 'true' predictor of age.

Sources of error

A variety of errors reduced the accuracy of age prediction, and therefore increased the width of the confidence intervals of the predicted age of whales. As pointed out by Angliss *et al.* (1995), biases in photogrammetry of cetaceans fall into two main categories. A combination of errors associated with photograph quality and reader error (technical biases), and the inherent inter-individual differences among whales (biological bias) increased the variability in age prediction in our study.

The best photographs were those taken at medium distance with the whale horizontal at the surface and perpendicular to the photographer, and showing one side of the entire rostrum back to the post-blowhole callosities. Deviations from this ideal affected the measurements in different ways (*cf.* Gordon 1990). Some of the most common problems related to photograph quality were: some endpoints were not visible (*e.g.*, the post-blowhole callosities were not in the frame or the front tip of the bonnet was underwater); the whale was tilted on one side and the angle did not allow one to visualize the rostrum's profile from a lateral perspective (especially important to determine the zenith); the whale was leaving or approaching the photographer, thus affecting longitudinal measurements; the image was backlighted and the whale was too dark to find the apex; the lower lips were not in the 'closed' position, thus affecting the measurements involving the apex, *etc*.

The determination of the apex had a considerable variability given that the highest point of the lower lip is usually not a discrete 'point' but a wider portion of the lip, *i.e.*, the apex could be placed forward or backward along the lip according to the reader's criterion. This variability in apex placement also affected the position of the isthmus. The isthmus-to-apex distance was included only in the model for whales with continuous callosity pattern.

In some cases, the position of endpoints such as the rear margin of the bonnet and the front margin of the coaming was difficult to determine due to cyamid infestation on the head (Kraus *et al.* 1986, Rowntree 1996). This tended to erroneously enlarge the apparent dimensions of callosities. In many close photographs the texture and color allowed the reader to discern between callosity tissue and cyamids, and the endpoints of the callosities used for the measurements were their true endpoints. In photographs taken from afar, the endpoints were considered to be in the midpoint of the cyamid 'ring' that surrounds the callosities (*i.e.*, the midpoint between what appeared to be callosity tissue and the external margin of the cyamid ring). In these cases, the final determination of the callosity outline was done using the composite drawing of each whale's identifying features in the catalog (Hamilton and Martin 1999).

The precision of the repeated measurements made by the readers in terms of CVs (Table 3) is consistent with the errors reported in similar studies that used photographs of baleen whales to estimate their size and age, where CVs ranged between 0.6 and 4.6%

(Cubbage and Calambokidis 1987, Best and Rüther 1992, Angliss *et al.* 1995, Spitz *et al.* 2000). Readers could also be trained beforehand to improve measurement precision.

A longer whale-to-photographer distance did not necessarily imply that the quality of photographs was lower than at closer distance. In fact, some photographs taken at longer distances were better than those where the whales were too close, because in the latter a higher angle significantly affected some measurements (*cf.* Gordon 1990). However, when whales were too far, the distances measured between points were small, and consequently the relative error in those measurements increased. As described by Best and Rüther (1992), Table 3 shows an inverse relationship between the size of the measurements and their corresponding CVs, indicating that the error made in finding the endpoints is stable and independent of the magnitude of the measurement involved.

One way to counter this problem, especially when measuring small traits (*e.g.*, island length, zenith measurements), is to increase the distance between the projector and the screen. This increases the size of the projected image and should reduce the error. Nevertheless, the benefit gained with a larger image size may not be worth the loss of image definition, which may in turn reduce precision. Measurement quality could be enhanced by digitising the photographs and using specialized software to take the measurements (*cf.* Angliss *et al.* 1995, Perryman and Lynn 2002). The use of three-dimensional imagery also allows for higher precision, but the added cost and/or logistical complications may outweigh the minor improvement (Cubbage and Calambokidis 1987, Angliss *et al.* 1995, Dawson *et al.* 1995).

Medium distance photographs (as defined in methods) should be preferred over ‘too far’ or ‘too close’, unless the close photographs were taken horizontally to the whale (*i.e.*, close to the water surface) to reduce the angle effect. To reduce the error due to distance when measuring sperm whales, Dawson *et al.* (1995) discarded stereo photographs taken from a boat at distances greater than 60 m for their analysis. Close photographs of right whales have the added benefit of allowing for better discrimination between callosity and cyamids, thus reducing this source of error when finding the endpoints of the traits being measured.

Although we did not formally quantify it, the largest contribution to the width of the confidence intervals of predicted age is likely to be the inter-whale variation in the traits measured. Whitehead and Payne (1981) found that the best measurements of body length and rostral length were only slightly better correlated than the worst measurements, concluding that deviations from the regression line were mainly due to variations between individuals and not to measurement errors.

When several photographs of the same whale are available for different years, multiple sets of measurements and multiple age predictions for the same individual can be obtained. This could increase the accuracy of age prediction for a given whale.

Conclusion

We have presented a benign, simple and inexpensive photogrammetric technique to predict the age of N Atlantic right whales based on shipboard photographs. The compatibility of shipboard and aerial photographs of N Atlantic right whales used for matching known individuals has been described by Kraus *et al.* (1986). A combination of shipboard and aerial photographs, when available for the same individuals, could lead to the development of a similar method to predict the age of whales from aerial photographs. This method could be applied also to southern right whales in the southern hemisphere, where research is based mainly on aerial photographs (Whitehead and Payne 1981; Best and Rüther 1992).

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FIGURES

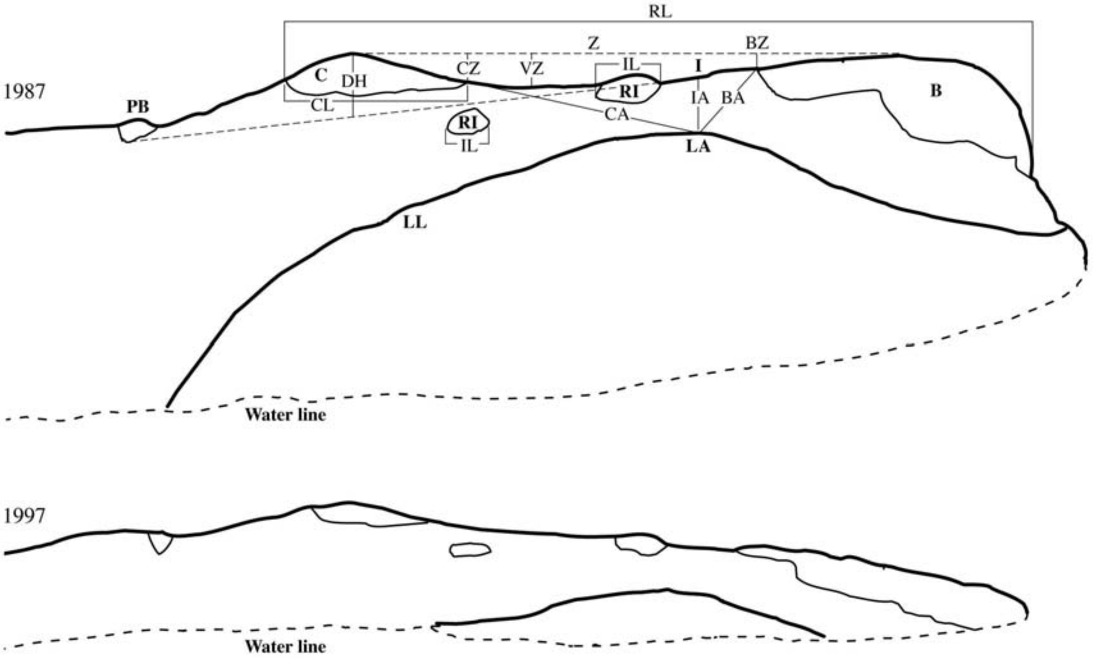

Figure 1: Traits of the head of a right whale and measurements taken on lateral photographs (see Table 1 for descriptions). *Traits*: B: bonnet; C: coaming; I: isthmus; LA: lip apex; LL: lower lip; PB: post-blowhole callosity; RI: rostral island; Z: zenith. *Measurements*: BA: bonnet to apex; BZ: rear margin of bonnet to zenith; CA: coaming to apex; CL: coaming length; CZ: front margin of coaming to zenith; DH: dome height; IA: isthmus to apex; IL: island length; RL: rostral length; VZ: valley to zenith. 1987: calf year; 1997: the same whale at age ten.

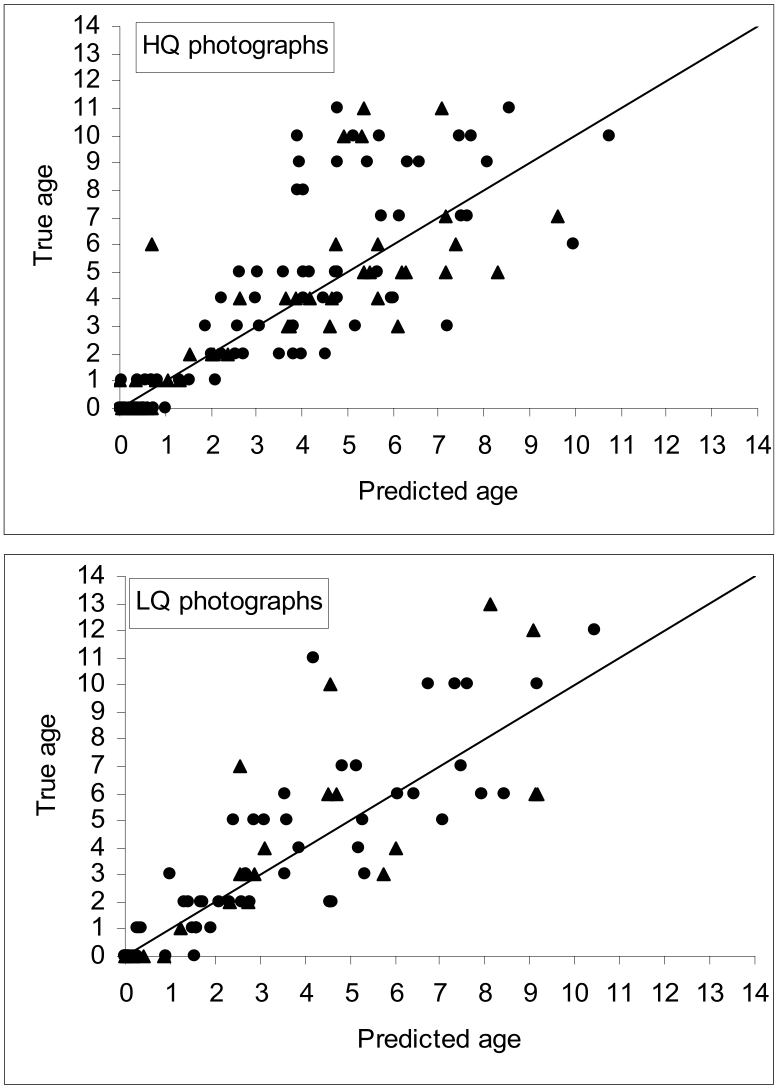

Figure 2. A comparison of true and predicted age (in yr) of females (●) and males (▲) in high quality (HQ) and low quality (LQ) photographs (slope of lines = 1).

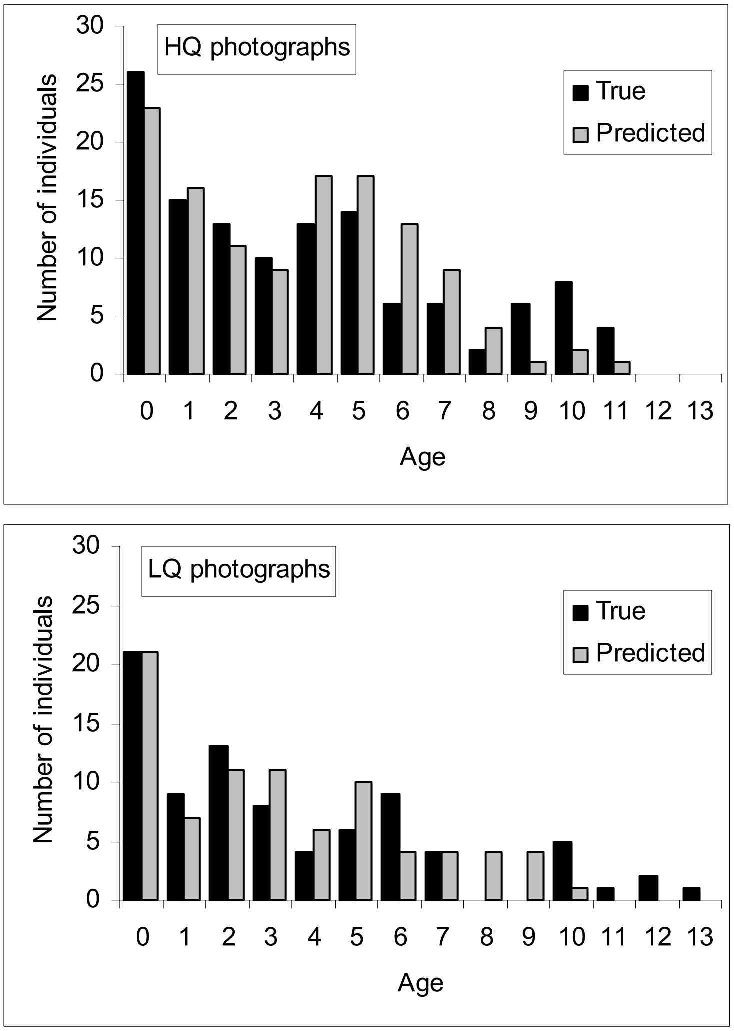

Figure 3. True and predicted age structures (in yr) of the populations of high quality (HQ) and low quality (LQ) photographs.

TABLES

Trait	Description
Dome	the raised portion of the rostrum where the coaming sits
Lip apex	the highest visible point of the lower lip on a lateral view
Isthmus	the narrowest point of the rostrum, determined by the intersection between the middle line along the rostrum and the perpendicular line to the lip apex
Valley	the lowest point of the rostral middle line on a lateral view
Zenith	the imaginary line that connects the highest point of the bonnet with the highest point of the coaming on a lateral view (used to describe the curvature of the rostrum)

Table 1: Traits of the head of right whales used for the measurements.

Sample	n	R^2	MSE	Variable	Estimate	SE	t	P
HQ	123	0.747	0.294	Intercept	2.201	0.366	6.02	**
				DH/CL	1.125	0.211	5.34	**
				(DH+VZ)/RL	-22.841	2.05	-11.14	**
				BZ/VZ	1.396	0.317	4.41	**
				CZ/VZ	0.821	0.374	2.19	*
LQ 1	50	0.795	0.269	Intercept	0.656	0.78	0.84	NS
				DH/CL	0.813	0.368	2.21	*
				(DH+VZ)/RL	-18.263	3.307	-5.52	**
				(BZ+CZ)/VZ	1.796	0.368	4.89	**
				DH/CZ	0.217	0.054	4.04	**
				DH/VZ	-0.218	0.052	-4.16	**
LQ 2	18	0.747	0.291	Intercept	2.221	0.53	4.19	**
				[(DH+VZ)/RL]/ [(BZ+CZ)/VZ]	-30.301	5.153	-5.88	**
				DH/BZ	0.435	0.092	4.71	**
LQ 3	15	0.89	0.246	Intercept	16.66	3.297	5.05	**
				(DH+VZ)/RL	-44.351	7.214	-6.15	**
				CZ/VZ	-10.278	2.827	-3.64	**
				DH/VZ	-2.013	0.668	-3.02	*
				DH/BZ	-0.629	0.15	-4.21	**
				(CZ/VZ)/(BZ/VZ)	5.329	1.529	3.49	**
Continuous	22	0.628	0.42	Intercept	1.844	0.717	2.57	*
				BZ/VZ	1.859	0.524	3.55	**
				CZ/VZ	-0.631	0.479	-1.32	NS
				(VZ+BZ)/CZ	-0.734	0.205	-3.57	**
				IA/RL	7.698	6.885	1.12	NS

Table 2. Age prediction models for high quality (HQ) and low quality (LQ, groups 1, 2 and 3) photographs, and for whales with continuous callosity pattern. MSE: mean squared error; SE: standard error. NS: non significant, P-value > 0.05; *significant, 0.01 < P-value < 0.05; **highly significant, P-value < 0.01. Abbreviations for the measurements used in the variables as in Fig. 1.

	Values			Reader effect			Whale effect		
Trait	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Island length	9.32	0.18	2.13	NS	NS	NS	**	*	**
Coaming length	30.92	0.24	0.90	NS	NS	NS	**	NS	**
Rostral length	138.06	0.39	0.31	*	NS	*	**	NS	**
Apex-isthmus	11.17	0.30	3.29	NS	**	NS	**	*	**
Coaming-zenith	3.96	0.16	4.11	*	NS	NS	**	*	**
Valley-zenith	4.57	0.15	3.61	NS	*	NS	**	*	*

Table 3. Average values of mean (in mm), standard deviation (SD) and coefficient of variation (CV, expressed as a percentage) for repeated measuremens for six traits. Significance values of the two-way non-parametric ANOVA with reader and whale as effect. NS: non significant, P-value > 0.05; *significant, 0.01 < P-value < 0.05; **highly significant, P-value < 0.01.

CHAPTER 5

PREDATION BY ORCAS (*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. Orcas (*Orcinus orca*) and southern right whales (*Eubalaena australis*) coexist off Península Valdés, Argentina. Since 1970, 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 involved no apparent behavioral changes in either species; in 37, obvious behavioral changes were seen; and in 12, actual attacks were observed. The orca / right whale ratio and the duration of encounters were minimum in the first type of encounters, and maximum during attacks. Most encounters occurred along the Eastern Outer Coast. The overall number of encounters decreased over the years. Orcas may assess right whale group size and their own group size before approaching and attacking. During encounters, right whales showed behavior patterns (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 abandonment of the Eastern Outer Coast by right whales lowered the number of encounters with orcas and consequently, the attack rate there decreased over time. At present it is not possible to determine whether predation pressure *caused* the change in habitat use by right whales. However, our data suggest that the "predation hypothesis" could partly explain the migration of southern right whales to this nursery ground.

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 (Tarpy 1979), the fin whale (Heide-Jorgensen 1988), the humpback whale (Whitehead and Glass 1985; Flórez-González et al. 1994), the gray whale (Baldridge 1972; Goley and Straley 1994; Ternullo and Black 2002), Bryde's whale (Silber et al. 1990), the minke whale (Guinet et al. 2000) 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 et al. 2002).

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 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 changed in the last three decades (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 through 2000.

Researchers recently debated on the effect 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 solo 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. Orcas are cooperative hunters (Guinet 1991) that can coordinate their predatory behavior to attack and even kill the largest predator, the sperm whale (Pitman et al. 2001).

In this paper we propose that if orca predation is an important evolutionary force acting on right whales, then right whales should exhibit behavior patterns that help to reduce predation risk. Also, we suggest that changes in the distribution of right whales at Península Valdés may be a response to the higher density of orcas along the EOC than in GN and GSJ.

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 to test this hypothesis worldwide.

MATERIALS AND METHODS

Study site. Right whales and orcas coexist along the shores of Península Valdés (PV), Argentina (42ºS, 63ºW), 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. We refer to the eastern portion of this section as the Eastern Outer Coast (EOC) (Fig. 1). The coast of the two bays alternates between regions with gradually sloping sandy or pebbled bottom beaches and vertical cliffs. Right whales at Valdés tend to be distributed close to shore along the 5 m depth contour (Payne 1986). The cliffs provide an exceptional setting to observe the whales from shore without disturbing their behavior.

Data collection and analysis. The term "encounter" refers to the simultaneous occurrence of orcas and right whales at the same site, 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). 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. Field notes from all observers were summarized, and data were collated and standardized to calculate descriptive statistics for duration, number of individuals and distance. Means ± standard deviations are provided in the text for descriptive purposes. 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 durations presented here underestimate actual durations.

Most encounters (111) were observed by the authors, while others (6) were reported by 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 (RB, JCL) lived on the EOC year round and made systematic observations of orcas and recorded their encounters with right whales. Other authors (GH, RP, MS) lived on GSJ year round or from August through November to study right whales during the peak of their calving season and also kept records of orca – right whale encounters. As a consequence, sampling effort (and chances of observing encounters) was similar and most intense in EOC and GSJ in those years during the time of peak abundance of right whales. Therefore, data from the EOC and GSJ collected in 1975-1982 and 1995-2000 were used to make comparisons of the changes in spatial and temporal distribution of the interspecific encounters. In Río Negro (RN) observations were made only during the 1990's.

Encounters were divided into three categories along a gradient of increasing activity of the animals and intensity of the encounters. Grade 1 encounters were characterized by the simultaneous observation of orcas and right whales in the same area, but no direct physical contact between the species and no apparent changes in their behavior were seen. In grade 2 encounters, orcas and right whales were in close proximity with potential physical contact. Behavioral changes and higher levels of activity were observed in both species, but no bites, blood or other evidence of a real attack were seen. 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 whale's body, or by blood or blubber on the water surface. Particularly detailed behavioral observations were made in some "case studies" described below.

Statistical tests were carried out using SPSS version 11.0.1 for Windows (SPSS Inc. 2001). Tests were two-tailed and the level of significance was set at $\alpha = 0.05$.

RESULTS

Group size and composition

We observed 117 orca – right whale encounters between 1972 and 2000. The total observation time recorded for 82 encounters was 2,272 min (mean=27.7 ± 45). At least 445 orcas and 291 right whales were involved in the encounters. The mean number of orcas per encounter (mean=3.8 ± 2.1) was significantly higher than the mean number of right whales (mean=2.5 ± 2.4) ($t=-4.87$; $df=115$; $p<0.001$), with a mean ratio of 1.5 ± 1.9 orcas per right whale in 116 encounters with known number of individuals.

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 ± 405 m. 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 from grade 1 to 3 (one-way ANOVA, $F_{(2,76)}=12.34$, $p<0.001$). The mean duration was 12.3 ± 22 min in grade 1 encounters, 27.6 ± 35.8 min in grade 2 encounters, and 81.1 ± 80.7 min during the attacks.

The average number of right whales per encounter (2.5 ± 2.4) did not vary with intensity of the encounters (Fig. 2). However, the average number of orcas increased with intensity of encounters from 3.3 ± 1.8 orcas in grade 1, to 4.5 ± 2.8 orcas in grade 3 encounters (Fig. 2). As a result, the orca / right whale ratio was greater in the 12 grade 3 encounters (1.8) than in the 63 grade 1 encounters (1.3) ($t=-2.12$; $df=73$; $p=0.038$).

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, 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 could not be determined.

During the 12 attacks, 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 took part in 87 (88.8% 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 known adult males were never positively identified during orca encounters with right whales. Adult female orcas and juveniles were recorded each in six (50%) attacks, but not necessarily in the same events. During attacks, orca group size ranged from one to nine. Solitary orcas attacked only on two occasions: both animals were adult males and they attacked solitary right whales in both cases.

Behavioral aspects of the encounters

Detailed information on the duration and behavior of both species was recorded during some encounters. The following “case studies” are the most representative descriptions of grade 2 and grade 3 encounters, and they 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. A summary of the behavioral patterns observed in both species during 18 encounters with detailed descriptions is provided in Table 2.

Case A. Obs.: RP. Grade 2. Camp Bay, GSJ, September 24, 1972, 13:13. From an aircraft circling over the whales in GSJ, two adult orcas, one male and one female, were followed visually as they swam along a line of right whale mother-calf (M/C) pairs near the shore and approached each of them. After the orcas left the whales, another observer on shore at the Cliff Hut (Katy Payne) saw several right whale females come together, form a ring with their heads directed toward its center ("rosette"), and thrash the water with their flukes. They maintained this star-shaped formation for about 40 min. One hour after the first sighting, two orca M/C pairs were spotted swimming synchronously in the same area. Two orcas approached a right whale M/C pair and subsequently left and approached them two more times, until the adult right whale made a lateral swish with her tail and both orcas left swimming offshore. The right whale calf pressed against its mother and both swam fast in water so shallow that they stirred a continuous track of mud. Another lone orca was seen passing by the head of another right whale mother but no further interaction was observed.

Case B. Obs.: JCL. Grade 3. Punta Norte, EOC, September 28, 1975, 16:30. About 45 min after catching a juvenile elephant seal by intentional stranding and feeding on it, a group of seven orcas (including one adult male) attacked a lone male juvenile right whale at 40-50 m from shore, biting its flanks, back, genital area and right fluke. As the right whale rolled repeatedly apparently trying to hit the orcas with its head, the orcas 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 patroled the shoreline as if searching for a potential seal prey. 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 was not seen before the attack. Petrels, gulls and cormorants pecked at the object, that appeared to be blubber and skin from the right whale. Visual contact was lost at dusk. At 1530 on Sep. 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 at a distance of 100 m from the right whales, most of the right whales formed a "rosette" with tails out and heads toward the center. The orcas swam through the formation and split the group of right whales apart. The right whales swam off in different directions. Then the orcas moved toward the previously attacked juvenile right whale who was 20 m from shore with another right whale. The other right whale fled when the orcas approached. The attacked juvenile was pushed by the orcas and attacked again on its front and sides. At 1610 the orcas left the area and returned at 1700, and approached the same juvenile right whale but did not attack. 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, 13:30. A lone adult right whale was seen flapping its tail vigorously on the water surface and then traveling extremely fast along the shores of Camp Bay in GSJ, while an adult male orca traveled in the same direction 30-40 m offshore of this right whale. Ten minutes later, the orca attacked the right whale, biting its right flank for about 30 sec. Then the orca bit on the right whale's jaw for about 15 sec, while the orca spun and twisted along its axis exposing its belly to the air. Then the orca separated from the right whale before attacking again and biting four more times. At this time, a kelp gull was seen pecking at the water around the whale as if it were feeding. After this, both animals moved out of sight behind a cliff.

Case D. Obs.: GH. Grade 2. Fracaso Bay, GSJ, September 9, 1982, 16:45. One adult male and at least five orcas of undetermined age were spotted in the same location where three right whales were swimming inshore. Many sea birds were feeding near them. Suddenly, one right whale sped forward with lots of white 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 could be recorded. The next morning a right whale calf was found dead on Fracaso Beach showing orca tooth marks and missing pieces of pectoral fins, tail flukes and skin.

Case E. Obs.: CG. Grade 3. Caleta Valdés, EOC, October 30, 1988, 11:30. Nine to 10 adult and juvenile orcas swam slowly to the S and approached a lone adult right whale traveling N 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, swished its tail and changed direction to travel southward. It was followed by the orcas for about 60 min, and attacked by three to four orcas at a time. 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 crossed their flippers as they swam and traveled along the shoreline to the N. At this point, the orca pack split and only the juveniles continued to follow the right whales for another 90 min. At 1400 the adult orcas rejoined the juveniles, separated them from the right whales, and all of the orcas then traveled S away from the three right whales, that continued moving N for 40 min.

Case F. Obs.: EI. Grade 3. Río Negro, September 6, 1996, 11:00. This encounter occurred in Punta Bermeja, a site N of Península Valdés that is part of the home range of the same orca population (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 vocalizations 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 that stayed at a distance of 700 to 800 m 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 PN 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 swishing their tails laterally. During the encounter the orcas split into two groups and merged several times: one group milled around the whales and the other moved about 100 m offshore and slapped their tails on the water surface before returning toward the whales. Ninety-five min later, two more adult right whales joined the harassed whales and formed a compact group, milling, arching their backs, keeping the calf in the center and staying at a distance of 20-80 m from the coastal reef. After the orcas left the area, the whales stayed at the same site for several hours, actively swimming in circles without changing location.

Case H. Obs.: MS. Grade 2. Cliff Hut, GSJ, October 13, 2000, 15:50. One adult male orca and one adult female or juvenile were spotted about 400 m offshore, milling around a group of 3 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 depth. One adult right whale kept actively pushing the calf with its head toward the center of the group. At 1615, almost the entire body of one orca was seen completely out of the water, immediately followed by the tail of a right whale. About one min later, one orca was seen swimming 100 m away from the whales, while the other orca was underwater. At 1620, both orcas were swimming away, 200 m from each other, when one adult right whale from the group initiated an extremely fast chase of one of the orcas. The whale stopped at a distance of 300 m from the orca, slapped its flippers several times on the water surface, rolled and returned to the group of right whales. Both orcas continued to swim away E mostly underwater, and were not seen again after this. At 1630 a right whale M/C pair coming from the W joined the group, and all whales stayed at the same site and were active at the surface. Five min later, two adults left, and the two M/C pairs remained close together for at least 45 min in very shallow water, keeping the calves in between them. No other right whales were seen in the area. A flock of kelp gulls hovered over the group throughout the encounter.

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 (χ^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 (χ^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 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 periods with most intense and comparable sampling effort are considered, 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 (χ^2=27.89; df=3; p<0.001).

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

During the 1996-2000 period there were on average 120 sightings of orcas per year off Valdés: 81% occurred along the EOC and the remaining 19% in other areas of the Peninsula. The mean number of orca sightings per month along the EOC varied throughout the year and had two seasonal peaks that are related to the abundance of sea lion and elephant seal pups (Fig. 4). The Sep - Nov peak (when orcas hunt for southern elephant seals), coincides with the time of highest right whale abundance in Valdés. The mean number of orca – right whale encounters per month in the EOC also varied during the year. In 1975-1982, the highest mean number of encounters (in Oct) was 2.8, but in 1996-2000 it decreased to 1.2 (in Nov). Also, in 1975-1982 the orca – right whale encounters occurred over eight months each year (May to Dec), but in 1996-2000 this "time window" of encounters was reduced to only four months (Aug to Nov) (Fig. 4).

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 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 (Tarpy 1979; Arnborn et al. 1987; Silber et at. 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 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).

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, pers. obs.) to 3.2 individuals (López and López 1985) on average while hunting for pinnipeds. 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.

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).

Orca behavior. *Appraising their prey*. Orcas did not approach the nearby right whales in over one half of the encounters (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 bites could be seen 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., Baldridge 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 charged, grabbed, and bit the right whale, females also charged but did not bite, and juveniles stayed at a distance. Case E also presents evidence of age 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 sampling 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. Right whales changed their distribution in Valdés, abandoning the EOC and moving 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 abandonded this area are less obvious. Rowntree et al. (2001) suggested 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. GSJ and GN have such sites and also have calmer water. If a "*relatively* lower predation risk is sufficient to favor migration" (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 near GSJ and GN where encounters with orcas are relatively less frequent. 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 during the last 30 years. The orca population 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 sighting frequency could indicate that orcas stopped visiting GSJ and concentrated their hunting effort in the more productive EOC. 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 (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).

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. 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 humpback whales reported bearing orca scars in Alaska and the NW Atlantic (Dolphin 1987, Katona et al. 1980) (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 more than very occasionally 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. Could attacks also occur at night? If future technology allows 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 (e.g., 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). In Valdés the mean orca group size is 3.2 (López and López 1985), compared to 9.3 (Dalla Rosa et al. 2002) and 27 (Hammond 1984) around Antartica. 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.

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 this 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 5 m 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 Valdés.

In summary, Península Valdés has features that are advantageous for right whales. Orca density and group size are relatively low compared to higher latitudes in the S Atlantic (López and López 1985; Dalla Rosa et al. 2002), it has growing colonies of pinniped prey for orcas (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 orcas. 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. 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 Península Valdés. 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 relative differences in orca predation pressure may affect right whale habitat choice, we are still far from understanding the causes for the observed changes in right whale distribution over the past three decades within this nursery ground.

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FIGURES

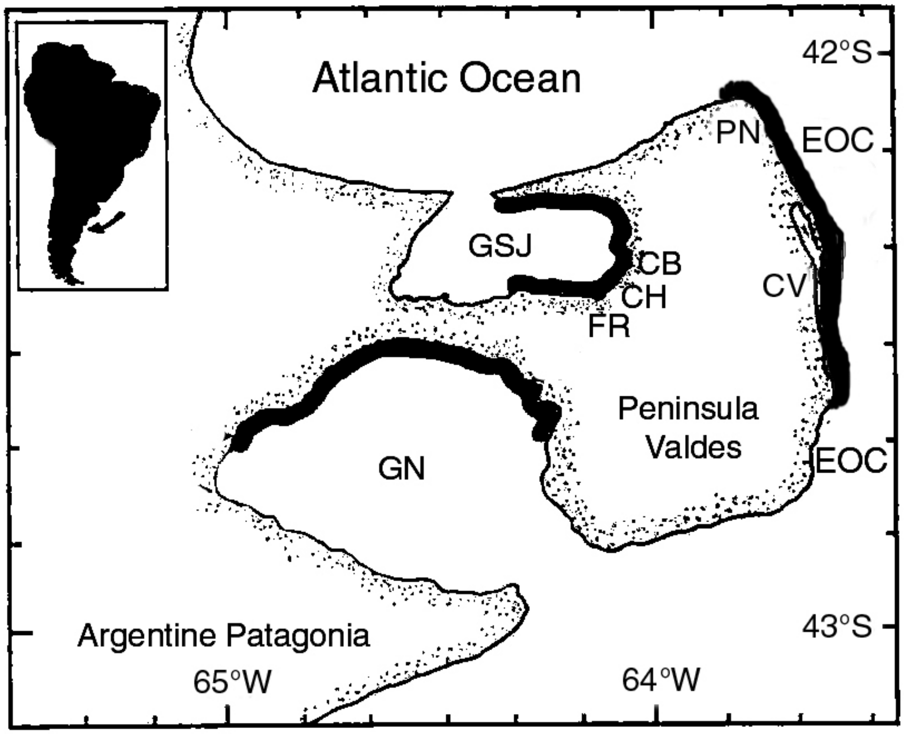

Figure 1. Map of Península Valdés showing the sites and the three areas where most encounters were observed. CB: Camp Bay; CH: Cliff Hut; CV: Caleta Valdés; FR: Fracaso; GN: Golfo Nuevo; GSJ: Golfo San José; EOC: Eastern Outer Coast; PN: Punta Norte. Shading indicates the regions of concentration of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

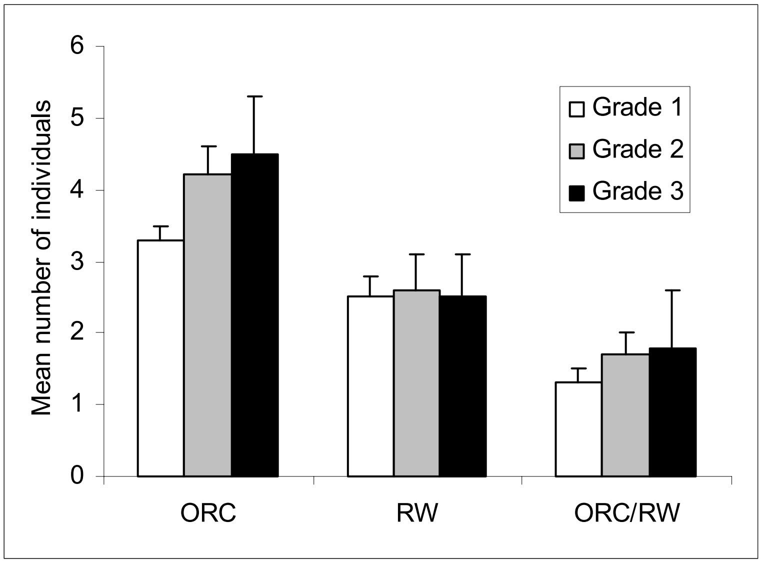

Figure 2. Mean (± SE) number of orcas (ORC), right whales (RW), and orca / right whale ratio (ORC/RW) in graded encounters.

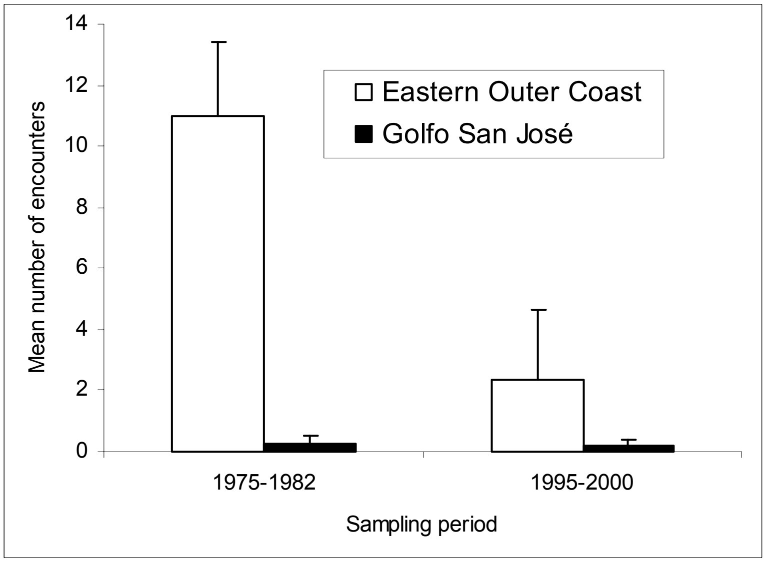

Figure 3. Mean (± SE) number of encounters per year in the two sites and the two periods with similar sampling effort.

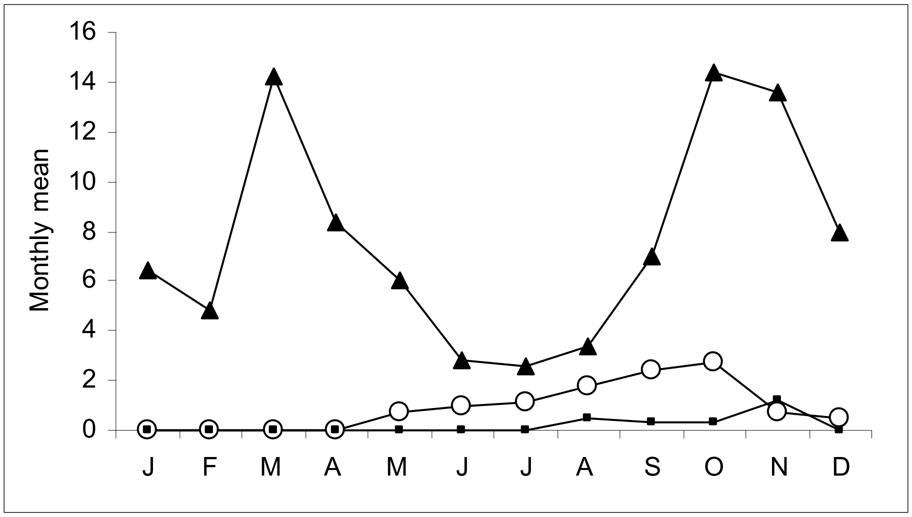

Figure 4. Mean monthly number of orca sightings in 1996-2000 (▲), and of orca - right whale encounters in 1975-1982 (○) and 1995-2000 (■) in the Eastern Outer Coast.

TABLES

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

Table 1. Percentage of encounters graded 1 to 3 (N=112) in which each age and sex class was observed.

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

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

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

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.

CHAPTER 6

KELP GULLS (*Larus dominicanus*) FEEDING ON SOUTHERN RIGHT WHALES (*Eubalaena australis*) AT PENÍNSULA VALDÉS, ARGENTINA: UPDATED ESTIMATES AND CONSERVATION IMPLICATIONS

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ABSTRACT

Kelp gulls (*Larus dominicanus*) feed on the skin and blubber of southern right whales (*Eubalaena australis*) at Península Valdés, Argentina, notably affecting the behavior of the whales. We studied these interactions during the 1999 - 2001 right whale calving seasons and updated the frequency of gull attacks through to 2002. Gulls did not direct their attacks evenly among all whale age classes. Mother-calf pairs received 81 % of the attacks and were attacked five times more often than juvenile whales. Juveniles spent over half of the time alone, and they received most of the gull attacks while they were solitary. However, the attack rate per hour was highest (5.2) when juveniles interacted with mother-calf pairs and lowest (0.7) while they were with adults. The attack frequency has continued to escalate since it was estimated in 1984 (Thomas 1988) and 1995 (Rowntree *et al*. 1998). In 1995, 12 % of 5-min intervals obtained during focal follows of mother-calf pairs contained attacks, compared to an estimated 26 % for the period 1999-2001 and 33 % in 2002. The increase in the proportion of whales with gull marks between 1974 and 2000 (from 1 % to 67.6 %) suggests that all whales at Valdés may have marks in the near future. Our results support the hypothesis that relatively few gulls specialize in feeding on whales. The local gull population has grown since the 1970's possibly as a consequence of the fish refuse available at fishery landfills. We provide recommendations for the management of the gull population to reduce its effects on right whale behavior and its potential impact on the calves' mortality rate.

INTRODUCTION

Kelp gulls (*Larus dominicanus*) at Península Valdés, Argentina eat the living skin and blubber of southern right whales (*Eubalaena australis*) (Thomas 1988). The attacks of gulls affect the behavior of whales, who respond by flinching and swimming rapidly away underwater (Rowntree *et al*. 1998). This flight behavior may increase the whales' energy expenditure, during a critical period when cows are fasting and calves are growing. This could potentially raise calf mortality (Rowntree *et al*. 1998). The parasitic behavior of kelp gulls on whales has not been observed in any other population, with the exception of two isolated instances recorded off the coast of Brazil (Groch 2001).

In the early 1970s, Cummings *et al*. (1972) reported that kelp gulls and brown-hooded gulls (*L. maculipennis*) landed on the backs of right whales at Península Valdés and pecked at their backs, possibly to feed on parasites. At that time, brown-hooded gulls took strips of peeling skin from the whales, but apparently the gulls did not feed on the whales' flesh (Rowntree *et al*. 1998). In 1984, Thomas (1988) saw kelp gulls actively eating peeling skin and the dermal and subdermal layers of mother right whales mostly in one bay at Península Valdés. In 1995, Rowntree *et al*. (1998) recorded gull attacks on whales of all age classes in at least three aggregation areas at the Península. Compared to undisturbed whales, mothers with calves under gull-induced disturbance spent about one-quarter of their day fleeing from gulls, and significantly increased the time they spent traveling at medium to fast speeds (Rowntree *et al*., 1998). At present, the parasitic behavior of gulls has become widespread at this nursery ground.

Gull attacks also affect the behavior of juvenile whales. Juveniles at Valdés spend one-fifth of their daylight hours resting at the surface and almost one-half of the time interacting with other whales (Sironi and Snowdon *in prep*.). Resting behavior and social interactions can be interrupted by the attacks, potentially affecting the social development of juvenile right whales.

In many regions gulls are considered a "problem species" due to the negative impact they have on other bird and mammal species (Yorio *et al*. 1998), water resources for human consumption (Dept. Environmental Protection 1998a), buildings and vehicles (Dwyer *et al*. 1996), and aircraft safety (Dolbeer *et al*. 1993). Gulls have varied and flexible foraging strategies (Pierotti and Annett 1990, Yorio *et al*. 1998, Bertellotti and Yorio 1999). Gull population expansion has been linked to the use of artificial food sources at waste disposal sites in France (Pons 1992) and in South Africa (Steele and Hockey 1990). Kelp gulls are the most abundant bird species feeding at urban and fishery waste landfills in northern Patagonia (Yorio and Giaccardi 2002). Most kelp gull colonies in Patagonia have increased in size between the late 1970's and mid-1990's (Bertellotti *et al*. 1995, 2001, Yorio *et al*. 1998). It is possible that the availability of abundant fishery refuse has enhanced the survival, breeding success and population growth of kelp gulls in the area (Bertellotti *et al*. 2001, Giaccardi and Yorio in press). The increase in gull attack frequency observed between 1984 (Thomas 1988) and 1995 (Rowntree *et al*. 1998) at Península Valdés may be a consequence of the growth of local kelp gull colonies during the same period.

In this paper we present frequencies of right whale-kelp gull interactions at Península Valdés updated to 2002. We compare these frequencies among whale age classes and provide temporal distributions of whales, gulls and their interactions throughout the right whale calving season for the 1999-2001 period. We discuss the interrelationship between whales, gulls, fishery waste and landfills. We suggest possible measures to reduce the frequency of the interactions and analyze the socio-economic implications of this conservation problem affecting Argentina's coastal wildlife.

MATERIALS AND METHODS

The interactions between kelp gulls and right whales were studied during the months of right whale peak abundance at Península Valdés (Aug to Nov) between 1999 and 2001. When Rowntree *et al*. (1998) studied the interactions in 1995, they concentrated their observation effort (79 %) on mother-calf pairs. Because the present study was part of a larger research project on the behavior of juvenile right whales, our observations were focused on juveniles, but data on abundance of all whale age classes at the study site were gathered. Individual whales were identified by their callosity patterns and back markings (Payne *et al.* 1983, Payne and Rowntree 1984). Data were collected from an Observation Hut located on a cliff top overlooking the ocean at 45 m above sea level in Golfo San José (42°25'S, 64°9'W).

We followed the methodology described by Rowntree *et al*. (1998) to estimate the frequency of gull attacks on juvenile whales. We used a 20X wide-angle spotting scope to visually follow individual whales and observe whether they were attacked by gulls. We defined a "gull attack" as any event during which the bill of a kelp gull contacted the body of right whales, most notably the portion of their back that is exposed to the air when the whales are at the surface. An "attack episode" was a sequence of attacks (or one isolated attack) that occurred with less than 5 min between attacks (Thomas 1988, Rowntree *et al*. 1998).

Continuous focal animal follows (Altmann 1974) of juvenile whales were divided into 5-min intervals (Rowntree *et al*. 1998). The occurrence of gull attacks was recorded using one-zero sampling (Altmann 1974, Martin and Bateson 1993). When an attack occurred, the corresponding 5-min interval during the follow was scored as 1; intervals that had no attacks were scored as 0. The percentage of intervals scored as 1 over the total number of intervals provided an estimation of the frequency of gull attacks (Rowntree *et al*. 1998) on right whales during follows. Using this methodology, we monitored gull attack frequency at the study site every year between 1995 (Rowntree *et al*. 1998) and 2002 (these data and several observers).

Right whales at Península Valdés have wounds on their backs that are probably caused by the repeated attacks of kelp gulls (Thomas 1988, Rowntree *et al*. 1998). These lesions are visible on photographs because they are mostly white on a black skin background. We analysed photographs of right whales taken during aerial identification surveys (Whale Conservation Institute data) in 1974, 1990 and 2000 to update the estimates of the percentage of whales with lesions for those years. During follows, we recorded whether attacks were aimed at the lesions or at smooth skin. The age class of the attacking gulls was determined by plumage and the percentage of adult *vs*. juvenile gulls was calculated.

Focal right whale juveniles were considered to be "social" when there were one or more "secondary" whales within a five whale-length (WL) radius from the focal subjects; otherwise, they were "solitary" (Sironi and Snowdon *in prep*.). Secondary whales were classified into four age classes: mother-calf pairs, adults, juveniles and whales of indeterminate age. The proportion of time juveniles were solitary or socializing with each age class was calculated from focal follows. We counted the number of times juveniles were attacked under the different sociability conditions and calculated the rate of attack per hour spent alone or socializing with each class during the follows that contained attacks.

Every hour we surveyed a 3.8 km-long and 2 km-wide strip of coast to count the number of whales and gulls present by instantaneous scan sampling (Altmann 1974). We recorded the age class of whales, their overall behavior, their sociability, and whether or not they were attacked by gulls during the scan. The four behavioral categories considered were surface activity (behavior patterns causing white water, such as rolling, flipper and tail slapping, breaching), travel (locomotion that resulted in a change of location), rest (motionless at the surface), and underwater (when whales were submerged and their behavior could not be recorded) (Sironi and Snowdon *in prep*.).

Attacks on cows and calves during scans were recorded as occurring “on the pair” and not on the individual member of the pair. As a consequence, mother-calf pairs are counted as one “whale unit” (and not as two individual whales) for the purposes of calculating the percentage of attacks that were aimed at all whale age classes. We counted kelp gulls at roosting sites on the beach and on mussel beds during the low tide to estimate the number of gulls that could potentially attack the whales. Because during scans we did not count the gulls flying or floating on the water, our counts underestimate the true number of gulls present at the study site. To analyze the seasonal trends of the whale-gull interactions, we divided the study period into 12 ten-day intervals and calculated the mean number of whales, gulls and attacks per scan for each 10-day interval.

RESULTS

Focal follows of juveniles and scans were collected during nine months in three field seasons (1999-2001), and gull attack frequencies on mother-calf pairs were obtained for 2000 and 2002. Between 1999 and 2001 we observed 154 juvenile right whales during 238 h of focal follows totalling 2,855 5-min intervals. During these follows, we observed

187 gull attacks in 126 episodes. During 1,077 hourly scans we counted 69,713 gulls (x = 64.7 gulls per scan, SD = 53.1, range = 0 – 340) and observed 652 gull attacks on 10,331 whales (including resightings) of all age classes (x = 9.3 whales per scan, SD = 3.8, range = 0 - 37).

Mother-calf pairs (considered as a unit) represented 41.2 % (3,013 pairs or 6,026 whales) of all whales counted in the scans, followed by adults (24.7 % or 1,807 whales), juveniles (22.6 % or 1,651 whales) and whales whose age could not be determined (11.6% or 847 whales). Gulls did not aim their attacks evenly among all whale age classes (Fig. 1). If we assumed that gulls attack whales of all age classes evenly, then we would expect to observe 41.2 % of attacks on mother-calf pairs, 24.7 % on adults and 22.6 % on juveniles. However, mother-calf pairs were attacked twice more frequently than expected. The majority of attacks (80.8 %) were aimed at mother-calf pairs, followed by 8.9 % of attacks aimed at juveniles, 8.4 % at adults, and 1.8 % at whales of indeterminate age (juveniles or adults). The observed distribution of gull attacks per whale age class was significantly different from the expected based on the age class distribution of whales ($\chi^2 = 426.2$, df = 3, $P < 0.001$) (Fig. 1).

Gull attack frequencies at Península Valdés have been estimated primarily on right whale mother-calf pairs since the study of Rowntree *et al*. (1998) in 1995. Because the majority of our continuous follows focused on juveniles, we could not compare gull attack frequencies on juveniles directly to those obtained for mothers and calves. However, we used the gull attack frequency obtained during follows of juveniles to estimate the frequency on mother-calf pairs based on the distribution of attacks among all age classes obtained during scans.

During scans, we observed 0.035 attack per juvenile whale (or 58 attacks on 1,651 juveniles) and 0.175 attack per MC pair (or 527 attacks on 3,013 pairs). This indicates that individual mother-calf pairs experienced gull attacks five times more frequently than individual juveniles. During focal follows, gull attacks on juveniles occurred in 5.2 % (148) of all 5-min intervals over the three year period (2.5 % of intervals in 1999, 7.4 % in 2000 and 6.3 % in 2001). Based on the 5-fold difference in the number of attacks observed on individual mother-calf pairs and juveniles during scans, we estimate that mother-calf pairs would have been attacked on 26 % of 5-min intervals during follows in the same period (12.3 % in 1999, 37.1 % in 2000 and 31.6 % in 2001). For comparison, gull attacks occurred in 42 % of 81 intervals in 2000 and in 33 % of 224 intervals in 2002 when we monitored the attack frequency on mother-calf pairs. Fig. 2 shows the frequency of gull attacks at the study site between 1995 and 2002.

Similarly, we used the number of attack episodes per hour of observation of juveniles to estimate the number of attack episodes per hour for mother-calf pairs. The attack episode rate per hour for juveniles was 0.53 for the three-year period (126 episodes in 238 h). We estimated mother-calf pairs experienced 2.65 attack episodes per hour during the same period.

A total of 142 attacks were observed during 42.7 h and 21.7 h of focal follows of juvenile females and males, respectively. During these follows, females and males spent most of their time alone (56 % and 61 %, respectively), and the remaining time they socialized with whales of all age classes. Female juveniles spent most of their socializing time with mother-calf pairs (57.2 %) followed by juveniles (25.7 %) and adults (17.1 %). Juvenile males spent most of their socializing time with other juveniles (63.6 %) followed by mother-calf pairs (31.3 %) and adults (5.1 %). Because juveniles spent most of the time alone, most attacks occurred while they were solitary (Fig. 3a). However, during these follows the attack rate per hour was highest (5.2 attacks / h) when juveniles interacted with mother-calf pairs and lowest (0.7 attacks / h) when juveniles were in groups containing adults (Fig. 3b). The attack rate during the four social conditions (*i.e.*, solitary or social with mother-calf pairs, adults or juveniles) was significantly different for females ($\chi^2 = 8.28$, df = 3, $P = 0.041$) and for males ($\chi^2 = 12.4$, df = 3, $P = 0.006$).

We could determine where the gulls' bill contacted the body of right whales in 115 attacks. Gulls aimed 90.4 % of the attacks at the existing lesions on the whales' backs and the remaining 9.6 % at apparently smooth skin. The percentage of whales with lesions increased from 1 % in 1974 (Rowntree *et al.* 1998) to 37.8 % in 1990 to 67.6 % in 2000 (Whale Conservation Institute data). Most gulls (80.2 %) that fed on the whales were adults and the remaining (19.8 %) were juvenile gulls.

The number of whales, gulls and their interactions varied throughout the season (Fig. 4). The number of right whales and gulls per scan was highest (12.8 and 114.8, respectively) between Sep 25 and Oct 4 in the three years of the study. However, there was no significant correlation between the number of whales and gulls at the study site throughout the 12 ten-day intervals of the season (Pearson correlation = 0.35, N = 12, $P > 0.05$) (Fig. 4a). The correlation was also non-significant when only mother-calf pairs were considered (Pearson correlation, $r = -0.17$, N = 12, $P > 0.05$). A small proportion of the gulls that were visible at any one time were involved in the attacks (Fig. 4b). The abundance of gulls was positively correlated with the number of attacks observed during scans (Pearson correlation, $r = 0.77$, N = 12, $P = 0.003$) (Fig. 4b) and negatively correlated with the percentage of gulls attacking whales over the total gulls counted (Pearson correlation, r = -0.74, N = 12, P = 0.006) (Fig. 4c). After Oct 4, the number of whales decreased gradually while the number of gulls plummeted and the percentage of gulls involved in the attacks increased (Fig. 4a,c).

DISCUSSION

Because the attacks occur at a time when right whale mothers are fasting and calves are growing, Rowntree *et al.* (1998) suggested that intense gull harassment could compromise calf survivorship in the Península Valdés population. Our observations confimed that the majority of gull attacks were aimed at mothers with calves. This preference for mother-calf pairs can be due to a number of reasons. Calves need to breathe more frequently than adult whales and thus, they spend more time at the surface and are more exposed to the attacks; calves may have softer skin than adults; mothers and calves tend to swim closer to shore than other age classes (Payne 1986) and so they are the first whales that gulls encounter when they fly from shore to feed on the whales; and the larger "patch size" represented by the two whales in mother-calf pairs may be more attractive for the gulls than solitary whales. A combination of these factors may explain the higer frequency of attacks on mother-calf pairs than on other whale age classes.

Mother-calf pairs return to pre-attack behavior after between 30 and 60 min following an attack, spending 24 % of their daylight hours under states of gull-induced disturbance (Rowntree *et al.* 1998). Assuming that juvenile whales experience a similar recovery time, then we speculate that juvenile right whales spend 4.8 % of their daylight hours under gull disturbance. This suggests that the impact of gull attacks may be less severe on juvenile whales than on mothers and their calves.

However, our data revealed that gull attacks may affect processes that are important for the normal development of juvenile whales. For instance, on one occasion a juvenile female approached and interacted with five different mother-calf pairs over the course of 70 min. Three of the five interactions stopped after kelp gulls attacked the groups and the juvenile female subsequently left the cows and calves. The rate of harassment on juvenile females was almost three times higher when they interacted with mother-calf pairs than when they were alone. If juvenile females spend less time with mother-calf pairs and more time alone to seek relief from gull harassment, then the time juvenile females have available at Valdés for potentially learning important behavior such as maternal care (Sironi and Snowdon *in prep*.) will be reduced. This may affect their future maternal skills.

The intensity and high frequency of kelp gull attacks on southern right whales are unique to Península Valdés (Rowntree *et al*. 1998, Groch 2001). The updated estimates presented in this study indicate that the attack frequency continues to escalate with time. Based on our estimation of attack episodes per hour on mother-calf pairs, the incidence of attacks for the period 1999-2001 grew 11 times since 1984 and 2.3 times since 1995 (Thomas 1988, Rowntree *et al*. 1998). In 1995, 12 % of 5-min intervals obtained on mother-calf pairs at the study site contained attacks, compared to an estimated 26 % for the period 1999-2001. Gull attack data were collected from mid-September through late November in 1999 and from early August through late October in 2000. As shown in Fig. 4, the number of gulls present at the study site during most of the sampling period covered in 1999 is notably lower than during the period covered in 2000. This may explain the sudden difference in gull attack frequency between the two years. The dramatic increase in the proportion of whales with gull marks since 1974 suggests that potentially all right whales at Valdés will have gull marks in the near future.

Recent surveys along the Argentine coast identified 104 kelp gull colonies totalling 75,000 breeding pairs (Yorio *et al*. 1999). Most of the colonies whose size has been monitored have expanded during the 1980's and 1990's at rates of 6.4 to 58 % annually, including the colonies at Península Valdés (Bertellotti 1998, Yorio *et al*. 1998). The population growth of the largest breeding colony in Valdés (Isla de los Pájaros) has been attributed to the kelp gulls regularly foraging on fish waste at nearby local landfills, which probably enhances gull survival during the winter and increases life-span and breeding performance (Annett and Pierotti 1999, Bertellotti *et al*. 2001).

The causes of the increase in gull attack frequency are not evident. There are enough alternative food sources for the gulls in northern Patagonia other than whale skin and blubber. The gull colony at Isla de los Pájaros is surrounded by relatively rich intertidal areas with abundant invertebrates that are part of the natural diet of kelp gulls at other locations (Bertellotti *et al*. 2001). The fish discards produced by local fisheries in Golfo San Matías (adjacent to Península Valdés) could potentially support over 30,000 gulls; however, less than 8,500 kelp gull pairs breed there (Bertellotti and Yorio 2000). Therefore, there must be nutritive benefits for the gulls that prefer whale skin and especially blubber over other foods. Over 90 % of the attacks observed were aimed at the open wounds on the whales' backs, indicating the gulls' preference for the blubber over the skin.

Conservation implications

Right whales are the main tourist attraction in Península Valdés. Over 73,000 tourists went whale watching there in 1997, generating revenues of over US $15 million (Rivarola *et al*. 2001). The disturbing sight of right whales flinching violently and swimming away after kelp gulls have pecked on their backs to feed has become very common at Valdés. There is substantial popular support for the whales in Argentina. Consequently, pressure from the general public and from whale-watch tour operators to reduce the levels of gull harassment on the whales is increasing.

In September 2002, right whale and kelp gull researchers met for two days in the city of Puerto Madryn to elaborate a diagnosis of the interactions between the two species, their effects on right whales, and to explore potential solutions to reduce the frequency of the interactions (EC/FPN/ICB 2002). A major concern was the fact that it is not known if the majority of the gulls feed on the whales infrequently or if there are few specialists that feed on them frequently.

Our results appear to support the specialist hypothesis. The reduction in the number of gulls at the study site after October 4 is likely the result of nest attendance at the gulls' breeding colonies (Giaccardi and Yorio in press). The dramatic increase in the percentage of gulls involved in the attacks following the decrease in gull numbers after October 4 suggests that potential specialists remain in the area longer and continue to feed on the whales after most other gulls have left toward their nesting colonies to breed. If only specialist gulls feed on whales, then one would expect a relatively constant number of gulls attacking throughout the season (and relatively independent from the total number of gulls) for as long as the whales are present. Some gulls that feed on the whales may also leave the area in early October following the movement of most individuals. This would explain the decrease in the absolute number of gulls involved in the attacks after October 4.

The specialist hypothesis is also supported by the fact that very few of the gulls that are visible in one area have been observed attacking the whales at any one time since the problem was first studied in 1984 (Thomas 1988, Rowntree *et al*. 1998, this paper). Nine whales and 65 gulls were counted on average in each scan. However, we rarely observed two or more whales under attack simultaneously, suggesting that the relative abundance of whales is not a limiting factor for the attack behavior of gulls to occur. In contrast, virtually all gulls present were seen feeding at the intertidal areas during the low tide. Rowntree *et al*. (1998) found that gull attacks were relatively less frequent at low and rising tides. Nearly 20 % of the attacking gulls were juveniles, indicating that the gulls have the ability to learn this behavior early in their lives and relatively rapidly. If the parasitic behavior began in the 1970's, then it could be argued that enough time has passed for most or all gulls in the population to have learned the behavior. Yet, few gulls display it at any one time. The current percentage of adult *vs*. juvenile gulls that showed the attack behavior reflects the age structure of the overall gull population (Bertellotti and Yorio 2000).

Although we did not quantify this, it appears that relatively more whales have few or no gull marks late in the season (late Oct through Nov). If this is true, then by migrating to Valdés later in the season right whales may benefit from lower levels of gull disturbance. A shift in the timing of peak whale abundance could be indicative of this possibility, that is supported by the dramatic drop in gull abundance that we observed in early October. Obtaining conclusive data to support or reject the specialist hypothesis is relevant to propose effective conservation measures to reduce the frequency of the interactions between gulls and whales.

Management recomendations

Managing the problem of right whale – kelp gull interactions at Península Valdés is challenging for several reasons. Both species are native to Patagonia, the interactions occur within a protected natural area where right whales are the main tourist attraction, there is a strong public pressure to solve the problem, and there is an important economic component associated with the local fishery industry and with the management of urban and fishery landfills by the government.

In 1998 the International Whaling Commission held a Workshop in South Africa to assess the worldwide status of right whales (IWC 2001). Among the factors potentially affecting the recovery of right whales, the workshop recognized that "kelp gull harassment of right whales off Península Valdés, Argentina (Rowntree *et al*. 1998) has grown substantially worse in parallel with increasing areas of open waste disposal sites and a concomitant growth in gull populations. Avoidance reactions of the whales significantly impact their behavior and perhaps their distribution. The workshop recommends that these disposal sites be aggressively regulated" (IWC 2001).

The participants at the 2002 Workshop in Puerto Madryn (EC/FPN/ICB 2002) proposed the following preliminary recommendations to reduce the frequency of the interactions.

Reducing the food available to gulls by improving waste management practices at landfills (covering the fish refuse, recycling, incineration) and reducing fishery discard offshore should be priorities (Yorio *et al*. 1998, Giaccardi and Yorio in press). The Workshop recognised that a reduction in the available food from fisheries could induce more gulls to feed on whales at least temporarily.

Gull culling is not recommended at present until the specialist hypothesis can be confirmed. The removal of specialist gulls could reduce the frequency of the interactions. However, the actual proportion of the gull population that feeds on the skin and blubber of living whales cannot be estimated unless a project involving artificially marking gulls is developed.

Gull dispersion methods at landfills (habitat alteration, propane cannons, gull distress calls, trained dogs, pyrothecnics) (Dept. Environmental Protection 1998b) should be explored. Kelp gulls at the urban landfill in Puerto Madryn appear to be dispersed by human and dog presence and by frequent fires set to burn waste (Giaccardi and Yorio, in press).

Research to monitor the frequency of whale – gull interactions and the population dynamics of both species should be supported and continued. Monitoring the interactions should be done around the same dates each year (preferably during the peak concentration of right whales in Sept) to avoid biases due to seasonal variations.

FUTURE AIMS

Kelp gull attacks increase the energy expenditure of right whale mothers and calves (Rowntree *et al.* 1998). This may affect the normal growth of the newborn calves and could potentially raise infant mortality rates (Rowntree *et al.* 1998) as evidenced by dead calves stranding on the beaches of the nursery ground. If this is in fact true, we need to provide evidence of this effect to the decission makers in Argentina to foster the implementation of effective conservation measures to reduce gull harassment on right whales in Patagonia.

In order to understand the possible connection between gull harassment and right whale mortality rates, it is necessary to find answers to the following questions. Were the Península Valdés right whales healthier in the 1970's than in the 1990's? Are the individual right whale mothers and calves whose backs are not scarred by gull attacks healthier than those that have many gull marks? Are there differences in nutritive condition between the right whales at the nursery grounds off Valdés and off South Africa? Gull attacks do not occur in South Africa (Rowntree *et al*. 1998), and strandings of dead right whale calves are less frequent than at Península Valdés. To answer these questions, we should evaluate the nutritive and health condition of right whales over the past three decades and correlate it with the annual number of dead calves and with the changes in the incidence of gull attacks over time.

One way to do this is by analyzing the long-term photographic record of the Península Valdés right whales obtained during annual aerial surveys of the population since 1971 (Whale Conservation Institute). Changes in the nutritive condition of gray whales associated with fasting during the nursing season can be detected by taking measurements of body length and width on aerial photographs (Perryman and Lynn 2002). It is possible that this technique could be applied to right whales to explore trends in their nutritive condition since 1971 to the present. Similarly, comparisons could be made between the Argentine and South African right whale populations. The extended sighting histories and photographic record of known individuals could allow us to detect changes in their nutritive condition in the past three decades. This could alert us of potential variations in the overall health of the population. These data could be complemented with measurements of blubber thickness of whales stranded at the Península that are being collected at present (WCI / FPN) and with available observations of activity patterns, blow intervals and body condition of mother-calf pairs at Península Valdés (Rowntree, unpubl. data).

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FIGURES

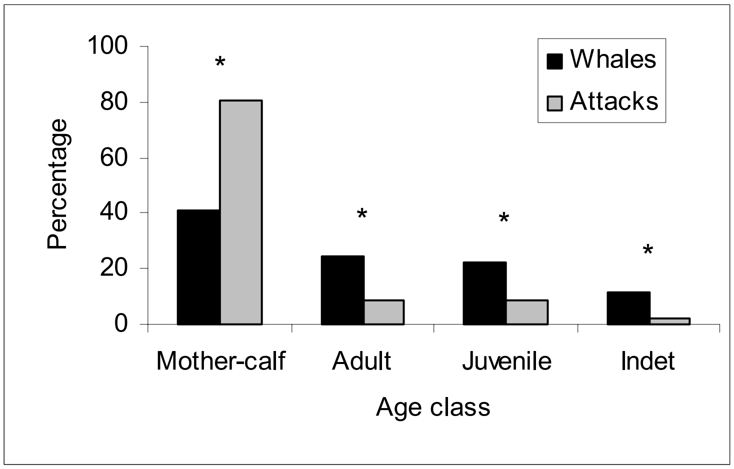


Figure 1. Age class distribution of right whales at the study site and percentage of gull attacks aimed at each age class. The two distributions are significantly different (χ^2 = 426.2, df = 3, P < 0.001).

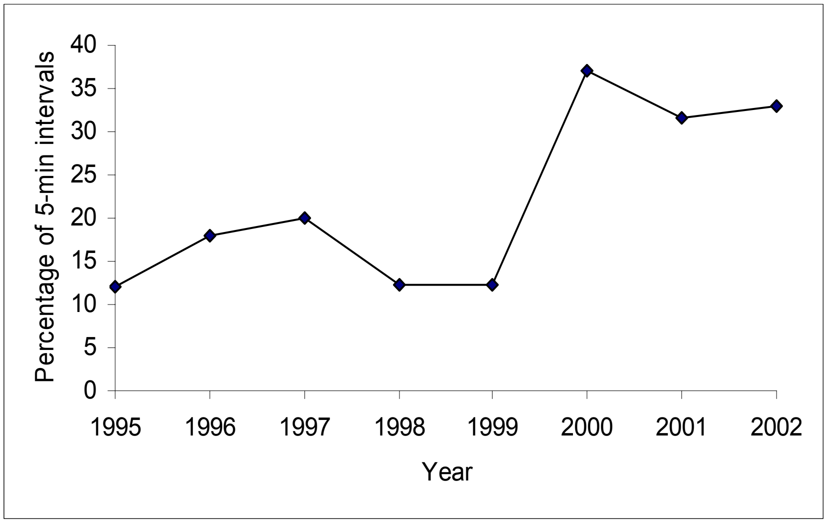
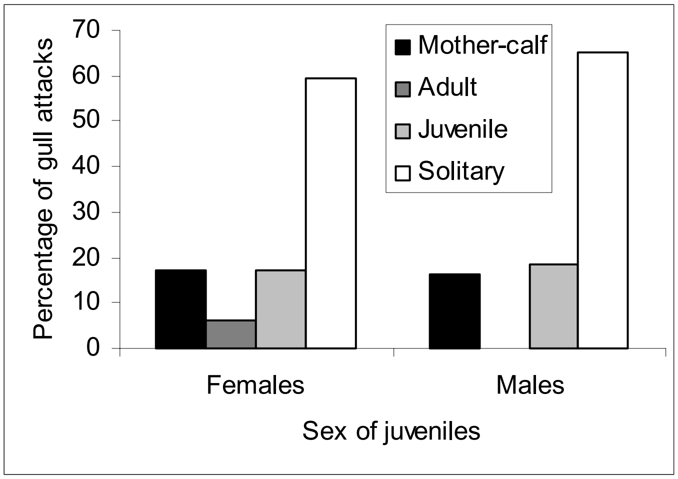
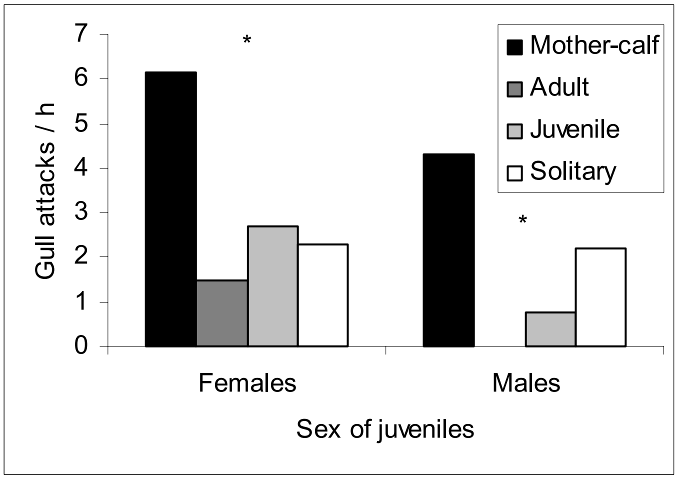


Figure 2. Annual percentage of 5-min intervals with gull attacks during focal follows of right whales at the study site. 1995: from Rowntree *et al*. (1998). 1996-1998 and 2002: several observers. 1999-2001: based on extrapolations from this paper (see text for explanation).



(a)



(b)

Figure 3. Percentage of gull attacks (a) and gull attack rate per hour (b) on juvenile females and males during their social interactions and solitary time. The attack rate per hour was significantly different from an even distribution for females ($\chi^2 = 8.28$, df = 3, P = 0.041) and for males ($\chi^2 = 12.4$, df = 3, P = 0.006).

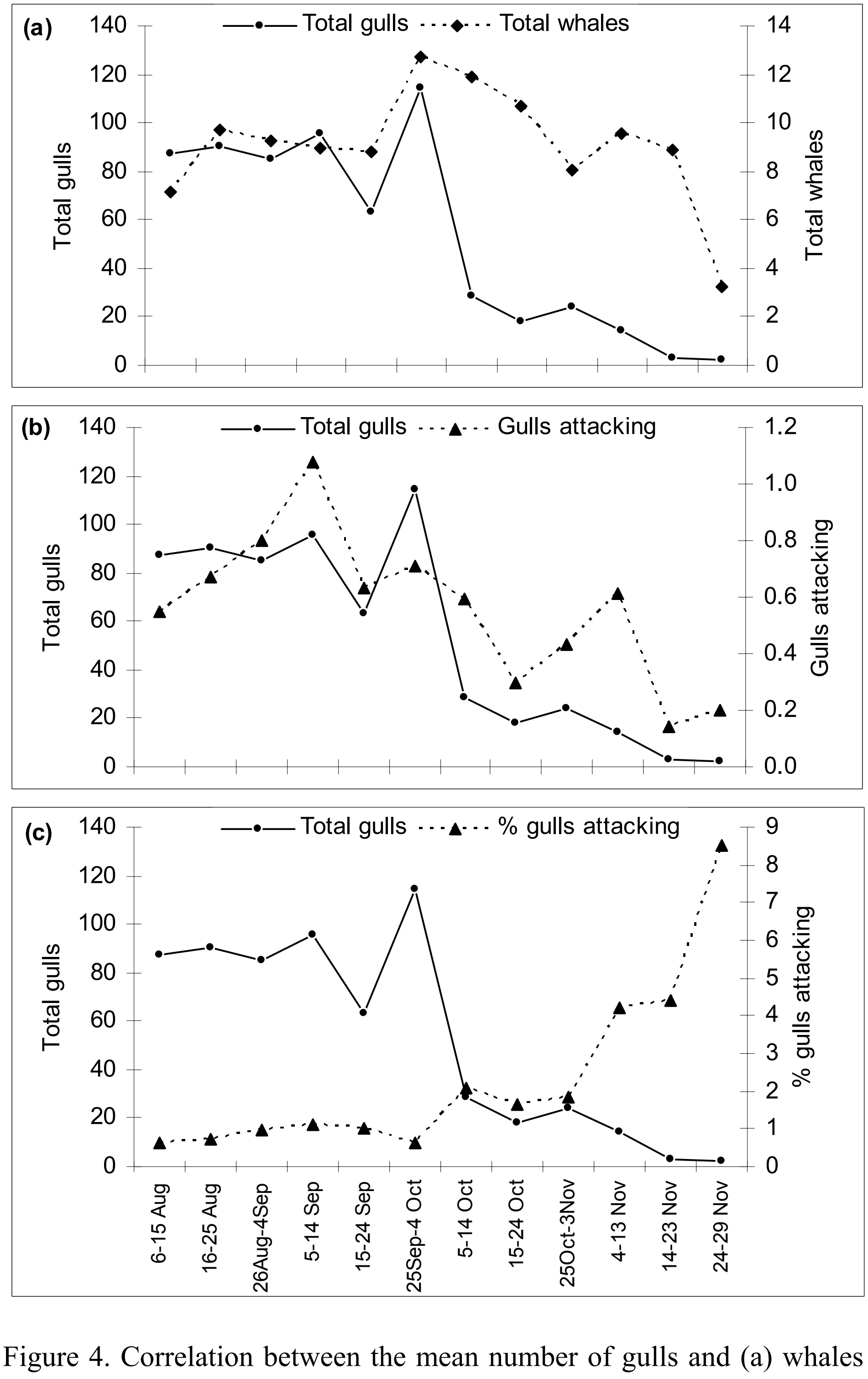


Figure 4. Correlation between the mean number of gulls and (a) whales (r = -0.17, N = 12, P > 0.05), (b) gull attacks (r = 0.77, N = 12, P = 0.003), and (c) percentage of gulls attacking whales (r = -0.74, N = 12, P = 0.006) per scan per 10-day interval.