Long-Term Population Trends of Patagonian Marine Mammals and Their Ecosystem Interactions in the Context of Climate Change

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Species Assemblage

Marine mammals that live in the Patagonian shelf include several species of pinnipeds and cetaceans, most of which extend their distribution ranges to tropical or subtropical seas, through subantarctic waters, or beyond the shelf in deep ocean waters, all of them in the Southwestern Atlantic (SWA) ocean. The pinnipeds include the South American sea lion *Otaria flavescens*, the South American fur seal *Arctocephalus australis*, and the southern elephant seal *Mirounga leonina*, which live, feed, and breed in local populations in the Argentine sea or are part of larger distribution ranges (Crespo et al. 2007). Antarctic seals (crabeater *Lobodon carcinophagus*, Weddell *Leptonychotes weddellii*, and leopard seal *Hydrurga leptonyx*) and Antarctic *Arctocephalus gazelle* and subantarctic *Arctocephalus tropicalis* fur seals pass through the Argentine sea as erratic individuals (Crespo 2009).

Among cetaceans there are few species that use Patagonian waters for feeding and breeding, like the southern right whale *Eubalaena australis* and several species of small cetaceans like the dusky dolphin *Lagenorhynchus obscurus*, Peale's dolphin *Lagenorhynchus australis*, the common dolphin *Delphinus delphis*, the bottlenose dolphin *Tursiops truncatus*, and Commerson's dolphin *Cephalorhynchus commersonii* (Crespo et al. 2007). Like pinnipeds, some other cetaceans have wide or cosmopolitan distribution ranges but have local populations in Patagonian waters, i.e., the killer whale *Orcinus orca*, the pilot whale *Globicephala melas*, the false killer whale *Pseudorca crassidens*, the Risso's dolphin *Grampus griseus*, and several species of ziphiids very poorly known (Crespo et al. 2007, 2009). Eventually erratic

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individuals of hourglass dolphins *Lagenorhynchus cruciger* or Fraser's dolphins *Lagenodelphis hosei* may also appear in Patagonian waters.

The species' assemblage of top predators is completed with a number of species of marine birds, sharks, and rays that use the same prey species of fish and squid as marine mammals. Nevertheless, they will not be treated in the present chapter.

Ecological Characteristics of Marine Mammals

In most cases, marine mammals are close to the top of their food webs. They are considered to be K-strategists (Estes 1979; McLaren and Smith 1985). Their characteristics include large body size, long life spans, low reproductive rates, parental care, delayed reproduction, juvenile survival less predictable than that of the adults, and predictable adult survival. In some cases, they appear to show density-dependent responses in their population parameters (Fowler 1981, 1984; Doidge et al. 1984; Evans and Stirling 2001; Crespo et al. 2019). Some of these parameters for the cetaceans are tabulated by Lockyer (1984) and by Evans (1987). Among the mammals, they can be placed at one of the extremes of the r-K continuum; and at the other end, we find rodents and insectivores.

Marine mammals are long-lived species, with life span ranging from around 20 years for small dolphins and sea lions to 40–60 years in many species of seals, large delphinids, and whales. Females may produce at most a calf per year in species like seals, sea lions, otters, and cetaceans (Estes 1979; Riedman 1990). However, lower reproductive rates are found in the larger dolphins and whales, which may reach a calf every several years (Evans 1987). The breeding cycle in the southern right whale lasts between 3 and 4 years (Payne 1986; Payne et al. 1990). Adult size and weight may range from 1 m and 15 kg in the sea otter *Enhydra lutris* to 30 m and 100 MT in the blue whale *Balaenoptera musculus*. Sexual maturity is usually delayed in life. Most of the seals and sea lions, and several species of small cetaceans, attain sexual maturity 4 to 6 years after birth. Some larger delphinids and ziphiids begin to reproduce after 9 years or more (Lockyer 1984; Perrin and Reilly 1984).

Parental care includes long periods of lactation and teaching of swimming and techniques for prey capture. In many large odontocetes, calves remain in herds close to relatives for several years. Seals, on the other hand, have a shorter period of parental care, with the hooded *Cystophora cristata* and elephant seals *Mirounga* spp., at one extreme, having a period of care of less than 1 month, which is in part offset by the high rates of energy transfer between mother and calf during lactation (Riedman 1990).

Survival is relatively uncertain between weaning and sexual maturity. This period, while the individual is learning different feeding and reproductive behaviors, is usually critical, and mortality is frequently due to lack of experience. However, once the basic skills are mastered, life becomes more predictable (Caughley 1966; Barlow and Boveng 1991). Population parameters, such as age at sexual maturity and reproductive rates, seem to be density dependent, but there is still some ongoing controversy on the subject (Eberhardt 1977; Fowler 1981; 1984; DeMaster 1984; McLaren and Smith 1985).

Many species, such as large whales, otters, and some sea lions, have been driven to the edge of extinction. Many of them have recovered or seem to be recovering. In some baleen whales, the response to the reduction in negative impacts has been quick (Best 1993), but for others it has been argued that interspecific competition may slow down the process (see discussion in Clapham and Brownell 1996). This leaves open questions concerning the existence of density dependence and the role that other environmental factors may play in that recovery. The lesson, from an ecosystem management point of view, is that even resilient ecosystems may take decades to return to their previous conditions after major disturbances and that there is no certainty that they will return to the same conditions. It is possible to eliminate or mitigate negative impacts on an ecosystem, but it is not possible to predict the trajectory of the response or its endpoint.

The Use of Aquatic Mammals by Humans

Humans have utilized aquatic mammals since prehistoric times, and archaeological records indicate the existence of tools and weapons made out of bone or stone for the apparent purpose of hunting mammals. In the cold regions of the planet, the scarcity of animal protein of terrestrial origin, and of alternative food sources, led humans to exploit marine mammals on the coast or at sea (Bonner 1982). There were several characteristics that made marine mammals a very valuable resource. They (a) had a large amount of fat and protein, more concentrated than in fish or shellfish, thus providing a high-value diet; (b) were a source of fur and leather that served for covering in cold and humid environments; (c) were accessible to humans with a simple technology; (d) were predictable in their locations or in seasonal migrations; and (e) in the case of pinnipeds, were easy to catch because of their vulnerability on land or ice (Crespo and Hall 2001).

Some of these characteristics were of particular advantage with the pinnipeds or coastal small cetaceans, which are sufficiently large to provide an ample reward without serious problems or risks in hunting them (Bonner 1982). Since Paleolithic days, the hunting of seals and sea lions was a matter of survival and an activity of vital interest for many coast-dwelling communities in northern and southern Europe, Asia, South America, and other parts of the world. In some cases, the contribution of the aquatic mammals to the energy intake of some of these communities was very large. In aboriginal populations of southern South America, more than 90% of the total energy intake was provided by fur seals and small cetaceans (Orquera and Piana 1987; Piana 1984; Schiavini 1990).

A harpoon with a detachable head was developed and used in the Arctic and in southern South America (Fig. 1a, b) (Orquera and Piana 1987), developed and used by subarctic and subantarctic nomad aboriginal people. The head, made of hard

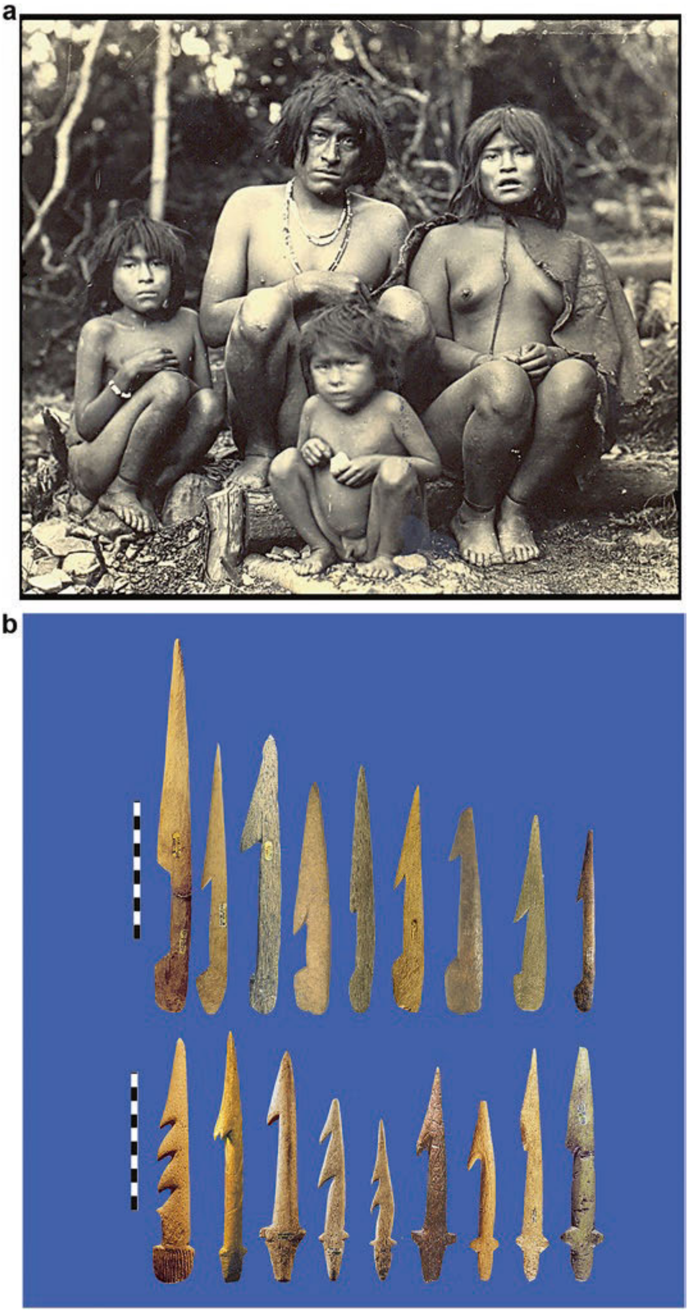

Fig. 1 (**a**) The photo of the Yamana family was taken by the *Mission Scientifique du Cape Horn* in 1881. (**b**) The harpoon line above are single shoulder base spearheads, typical of the last 3,000 years and in operation until the end of the nineteenth century. The bottom line are cruciform-based harpoon points, dated from about 7,000 to 5,000 years ago. (Scale in cm) (Courtesy of Luis A. Orquera and Ernesto L. Piana)

bone or ivory, was connected to a long stick. When the animal was harpooned, the head separated from the stick, but remained joined to a line and, in the case of the Inuit, to a float (avutang). The animal bled to death in the water and was eventually retrieved by means of the line and float. The harpoons varied from single sticks, with stone knives at the tip, to complicated technologies in the Inuit culture, but they all followed the same basic principles (Bonner 1982).

The economies of the sea-adapted people were extremely dependent on seal, sea lion, or cetacean products that were hunted or found stranded. The blubber was eaten, and, in areas with low access to wood, it was the main source of energy for cooking and used as fuel for lamps. According to Bonner (1982), the Inuit could have survived without the heat of the blubber lamps, but not without their light during the long Arctic nights. Prior to European colonization, subsistence hunting with a variable degree of intensity occurred along the entire Southwestern Atlantic coast (Orquera and Piana 1999; Gómez Otero 2007; Castilho and Simões-Lopes 2008; Bayón and Politis 2014; Borella 2014). This hunting pressure was considered low given past population abundance (Schiavini 1992; Orquera and Piana 1999; Zangrando et al. 2014). Fur seals were more frequent in archaeological sites than sea lions, possibly because of their availability in the environment. However, no record exists of the extent or rate of this harvest.

Whaling and Sealing in Modern Societies

The history of whaling as an industrial activity is much more recent (Evans 1987), although it remained a subsistence harvest for several centuries in the coasts of Japan, e.g., Baird's beaked whale *Berardius bairdii* fishery along the Sanriku and Hokkaido coast (Nishiwaki and Oguro 1971). The earliest recorded European whaling was carried out by Norse and Basque people in northwestern Europe and Spain, respectively. Norsemen caught whales off the coast of Tromsø as early as the ninth or tenth century, whereas the first data on whaling by Basque whalers dates from the year 670 in the Bay of Biscay. From there whaling spread to the rest of Europe, Greenland, and North America. At that time, during the sixteenth and seventeenth centuries, whaling became a major commercial operation quite different from subsistence activities. Northern right whales *Eubalaena glacialis*, bowhead *Balaena mysticetus*, and Atlantic gray whales *Eschrichtius robustus* were the main targets at that time and the first stocks to be depleted (Fig. 2). The Atlantic gray whale was soon driven to extinction (Allen 1980).

During the eighteenth century, whaling became established as an industrial activity and spread through the eastest coast of North America, the Indian and the Pacific oceans, and the subantarctic islands of the southern ocean. During this period, whaling was done using hand harpoons and rowboats, and the whales were processed alongside the boats. At this time, the Industrial Revolution resulted in a shift from a subsistence harvest to one based on monetary gain. The technological innovations brought about in those years, and the growing capital investment, resulted in more

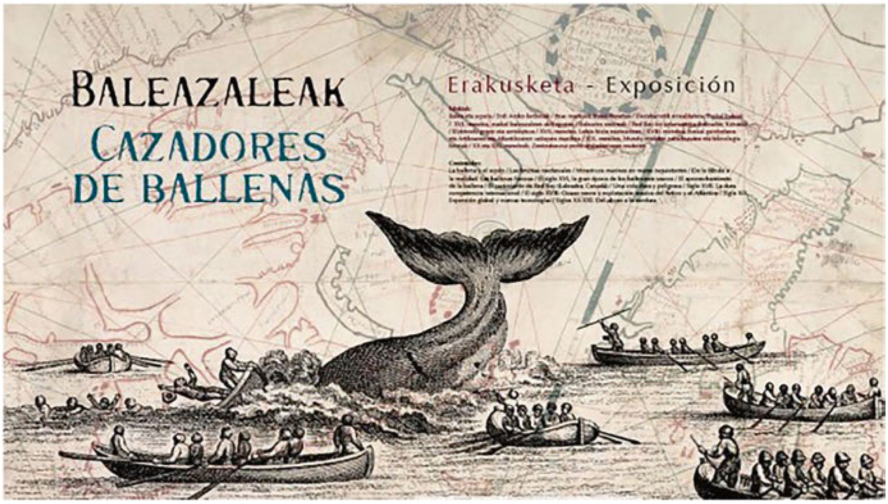

Fig. 2 Basque whalers catching a whale. (https://itsasmuseoa.eus/es/exposiciones/pasadas/40-baleazaleak-cazadores-de-ballenas)

efficient ways of hunting that led to the decline of several stocks. Right whales, fur seals, and sea otters, among others, started to decline during that period. Large rorquals and other species followed them later.

Modern whaling started at the end of the nineteenth century when the harpoon gun and the explosive harpoon were introduced and mounted on steam-driven vessels (Allen 1980). Fast-swimming whales like the rorquals, which were too fast for the rowboats, could now be taken with the new technology. This kind of whaling, with relatively minor changes, has also been used in the limited exploitation that took place until recent years.

Increasing demand and conceptual errors in terms of management, together with an intense competition for the resource, resulted in substantial declines in many marine mammal stocks. The history of whale catches shows that each target species was replaced by another one as the exploited stock was being depleted (Allen 1980; Evans 1987; Crespo and Hall 2001). The impacts of these harvests were probably very intense in some ecosystems, such as the Antarctic ocean, but they also affected other ecosystems visited by the whales during their migrations.

The long migrations of some aquatic mammals and other highly migratory species raise the issue of the ecosystem boundaries. Crespo and Hall (2001) wondered whether the management schemes for all ecosystems crossed by a major migration could be harmonized with respect to the migrating species and its impacts in each region's prey and competitors. Or should the definition of ecosystem, and therefore its management boundaries, be extended to include the whole migratory cycle? Practical reasons will probably decide the issue toward the first approach, but achieving harmony for all regions involved will not be easy, given the differences in priorities, economic standards, etc. The forum for this process may be, in the first stage, a combination of regional or national organizations when they exist and international bodies such as the International Whaling Commission – IWC (Crespo and Hall 2001).

Regarding sealing, it should be noted that, due to technological advances incorporated into the culture of aboriginal people, like fire guns, the original predator-prey relationship has been unbalanced over the last century. The possession of high-powered rifles and the ability to kill seals from a distance not only increased the number of animals hunted but also the rate of lost animals (i.e., wounded animals that were not recovered) (Bonner 1982). Smith (1987) estimated in 0.2% the annual ring seal lost by sinking in the harvest in the Canadian Northwest territories.

In the extreme South of America, in Tierra del Fuego, other human populations also sustained their economy based on pinnipeds. The channels and islands with a cold, wooded, and rainy environment were occupied until the last century by the Yámana, Halakwúlup (or Alacalufes), and Chono ethnic groups who, by their way of life, are collectively named as Canoe Indians (Orquera et al. 1979; Orquera and Piana 1983, 1984; Piana 1984).

The predecessors of these groups as early as 6000 B.P. were characterized by the intensive consumption of fur seals and sea lions (mainly the former and to a lesser extent the latter) and with less importance guanacos, birds, fish, and shellfish (Orquera et al. 1979; Orquera and Piana 1983, 1984; Piana 1984). A specimen of fur seal, due to its high caloric content, necessary to face the difficult climatic conditions in the area, would have provided around 200,000 calories, enough food for a group of 15 people for 3 days (Piana 1984).

In Patagonia, commercial exploitation started in 1790 when the Spanish Government created the Real Compañía Marítima establishing a whaling post at Puerto Deseado. That action was motivated by the fact that other European countries were pirating the resources in Patagonia. At least 16 right whales were taken during the first season, together with an undetermined number of sea lions and fur seals (Fig. 3). Nevertheless, the activity could not be sustained and whaling was abandoned soon, but the exploitation of pinnipeds spared and continued up to the end of the nineteenth century. Soon after the first Spanish expeditions, whalers and sealers of other nationalities, mostly British and American, started operating in the area. The peak of activity, particularly for whaling, peaked between 1820 and 1870. Sealers concentrated their activities in the Malvinas islands and Staten island. The rookeries located further north remained little affected or untouched. Because of its high-quality fur, the South American fur seal was the main target, although the South American sea lion and the elephant seal were also exploited for low-quality skins and oil (Bonner 1982).

In any case, from the eighteenth century on, an indiscriminate hunt for seals and whales began in the Southern Hemisphere. The southern fur seals were decimated together with the great whales, some of them reaching almost the brink of extinction, such as the Juan Fernández fur seal *Arctocephalus philippi* from the Juan Fernández islands, and the Antarctic fur seal from the South Georgia islands, where it was estimated that no less than 1,200,000 furs were extracted (Weddell 1825;

Fig. 3 Spanish soldiers killing sea lions. (https://fineartamerica.com/featured/spanish-soldiers-killing-sea-lions-the-gettyscience-photo-library.html)

Godoy 1963). Between South Georgia islands and Desolación island, 200 to 300 sailors and more than 2,000 tons of cargo moved by ships per year were occupied for the purpose of trade (Weddell 1825). A total of 320,000 sea lions and fur seals (and elephant seals that yielded 940 tons of oil) were hunted in the South Georgia islands alone between 1821 and 1822. According to Weddell, no less than 20,000 tons of elephant seal oil were transported to the markets of London since the islands were discovered to the date of his report.

The islands of the South Atlantic, as well as the coasts of Patagonia and Tierra del Fuego, with their numerous pinniped colonies, suffered attacks from whalers and sealers that entered the Argentine jurisdictional waters in search of skins, hides, and oil from these mammals during the last century (Godoy 1963), although this situation is prior to the May Revolution of 1810. According to the information provided by Spanish navigators in the period 1787–1791, there were many foreign ships that fished and hunted whales, fur seals, and sea lions on the Patagonian coasts (Ratto 1931). According to this last author, 14 ships were found in 1787, more than 30 in 1789, seven in 1790, and nine in 1791, all of them under the English, French, and North American flags. In addition to whaling, they landed to hunt sea lions, which was a clear territorial violation of the viceroyalty rights of that time.

A few examples of the Southwestern Atlantic that may be summarized will illustrate the situation here: the southern right whale, the South American sea lion, and the South American fur seal.

The southern right whale was one of the species of baleen whale that has been exploited for a long period in the "Brazilian Banks," the name given to the Southwestern Atlantic hunting area by the whalers. The first whales were taken around 1602 (Peterson 1948). By means of an extensive review of different bibliographical sources, the catch history of whaling for this species was reconstructed for the period 1670–1973. The model population trajectory indicates that the pre-exploitation abundance was around 30,000 to 35,000 whales (Fig. 4) (Romero et al. 2021). The abundance dropped to its lowest abundance levels in the 1830s when less than 1,000 individuals were left along the western South Atlantic ocean. Today, the current population abundance in that area is estimated to be around 5,000 whales (Cooke et al. 2015; Crespo et al. 2019), suggesting that the southern right whale population remains small relative to its pre-exploitation abundance (recovery level, 10–15%). During the 1960s and in spite that the species was protected nationally and internationally, 3,000 whales were taken in the Southern Hemisphere by illegal Soviet pelagic whaling operations, delaying the recovery of the species. Of those,

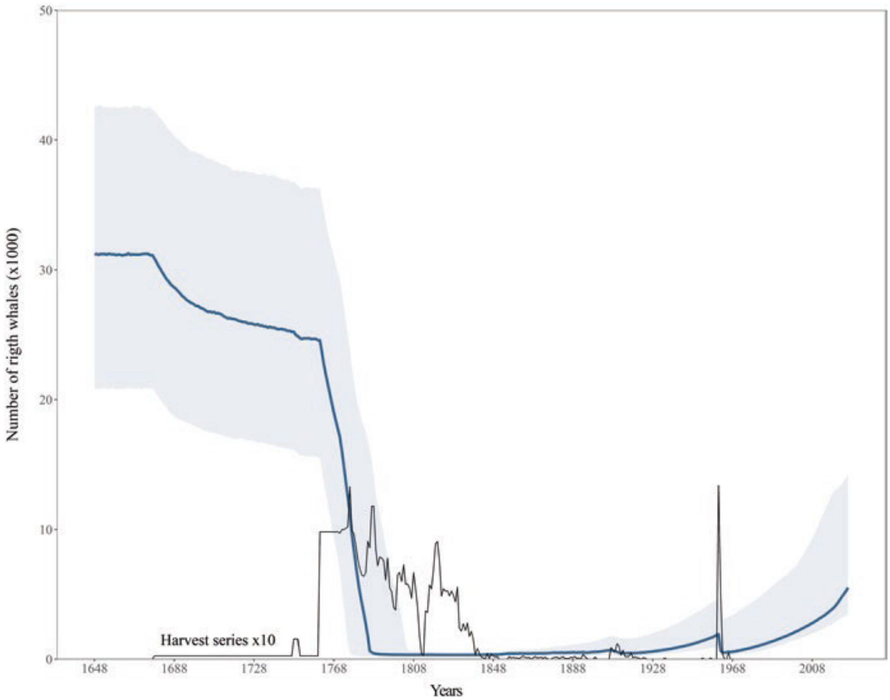

Fig. 4 Population trajectory of southern right whales in the Brazilian banks (blue line) and time series of catches (black line). The shaded areas correspond to the first and third quartiles. (After Romero et al. Subm.)

the number taken off Argentine waters was 1,356 and mainly during the 1961/1962 season (Tormosov et al. 1998). The results of the population dynamic modeling provide insights into the severity of whaling operation in the South seas and how the population responded at low densities and thus contribute to understanding the observed differences in population trends across the global distributional range of the species (Romero et al. 2021).

The South American sea lion is the most conspicuous marine mammal along the South American coasts, both Atlantic and Pacific, where it was heavily exploited. As a consequence of this exploitation, many of its colonies in the Argentine sea were decimated during the early twentieth century and nowadays show a clear recovery. As a K-strategist subject to exploitation, this population dropped to very low levels. After protection was imposed, recovery was at first very slow. After 50 years from hunting cessation, the population still represents only 35% of its pre-exploitation abundance (Fig. 5) (Romero et al. 2017). However, the opportunistic and plastic behavior of the South American sea lion, together with a high level of juvenile survival, resulted in a faster rate of population recovery in recent decades. Possible reasons for this improved survivorship may include an increase in the availability of food resources, prey switching, and a decrease in other causes of mortality (Romero et al. 2017). It was particularly interesting to understand how the population responded at low densities, how human-induced mortality interplays

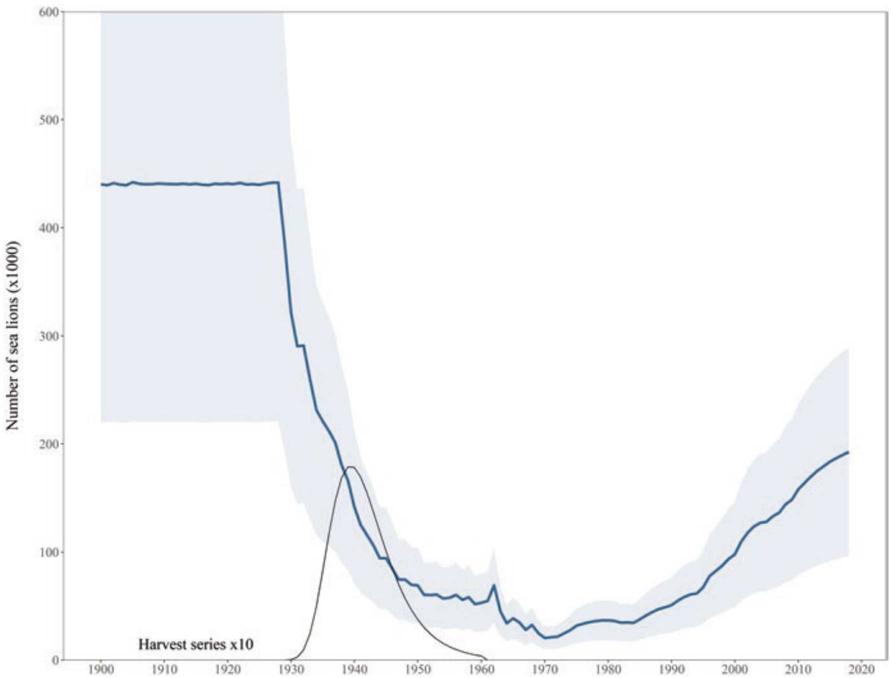

Fig. 5 Population trajectory of South American sea lions (blue line) and harvest series (black line). Shaded area indicates ± SD (after Romero et al. 2017)

with natural mechanisms, and how density dependence may regulate population growth. The population trajectory shows a nonlinear relationship with density, recovering with a maximum increase rate of 6%. Considering that the population of sea lions from this region holds around 72% of the species abundance within the Atlantic ocean, the population dynamic modeling provides insights into the potential mechanisms regulating the dynamics of South American sea lion populations across the global distributional range of the species.

The South American fur seal was heavily exploited from the nineteenth century until the end of the twentieth century throughout the South Atlantic coast, from Uruguay to Tierra del Fuego, the Malvinas islands, and Staten island, mainly for its skin and oil. In Uruguay, private concessions, and, later, the Uruguayan state killed at least 800,000 individuals between 1893 and 1991 (Franco-Trecu et al. 2019, and references therein). The exploitation in Uruguay lasted until 1991, while in Argentine waters the fur seal almost disappeared where 100,000 animals were taken in north and central Patagonia. These figures may include sea lions as well; nevertheless, they may be largely underestimated. The harvest closure in Uruguay probably led to a population increase that allowed to recover and repopulate the South Atlantic again. The rate of increase is currently around 8% per year, and several individuals tagged in Uruguay have been resighted in Patagonian waters (Crespo et al. 2015). Therefore, the Uruguayan fur seal population may not only be the largest of this species, but also helps to sustain the rapid growth of fur seals in the Argentine sea (Franco-Trecu et al. 2019).

The understanding of the underlying processes and comprehensive history of population growth after a harvest-driven depletion is necessary to assess the long-term effectiveness of management and conservation strategies.

A Change in Problems: Incidental Mortality and Competition for Resources Instead of Direct Catches

During the 1960s a major change started in the interactions between marine mammals and humans, a change that lasted for two decades at least. Almost at the same time that the direct catch of large whales was going down and the IWC promoted the moratorium for direct takes, incidental catch appeared as a huge problem with the development of many types of fisheries all around the world including gillnets, trawls, purse seiners, and longlines (Crespo et al. 1997; Crespo and Hall 2001). However, the interaction and the intensity was not the same with each type of gear. Perhaps the bigger problem arose with coastal species and gillnets, which mainly affected small cetaceans especially when the Food and Agriculture Organization (FAO) promoted the use of that fishing gear all around the World in less developed countries as a way to alleviate hunger. Nevertheless, the interaction with other gears like trawls should not be underestimated given the huge fishing effort and biomass extraction.

In northern Patagonia, as well as in waters of Buenos Aires province, Brazil, and Uruguay, gillnets became the most dangerous gear especially for the Franciscana dolphin *Pontoporia blainvillei*, a species which is thought to be in real danger given the high rate of incidental catch. The mortality of Franciscana in gillnets, mostly of juvenile individuals, is the most serious problem for the species throughout its distribution range, probably since the end of World War II (Fig. 6a, b). At that time, many artisanal fisheries for sharks developed from Rio Grande do Sul to Patagonia for vitamin A production, which was exported to Europe. Nevertheless, minimum mortality rates were always estimated around several thousands of individuals throughout the distribution range. Nowadays in Argentine waters, no less than 500 dolphins per year are taken (Crespo 2009). The estimated mortality for the whole distribution range could be around 1,200–1,800 individuals per year (Reeves et al. 2003).

Due to the variability found in mortality rates and abundance estimates, it is not known whether those mortality rates are sustainable (Crespo et al. 2010). In rough numbers, the upper limits of abundance estimations cannot account for the lowest estimates of mortality. Therefore, more precise estimates are needed along with conservation measures to preserve the species. Population viability analysis using data on abundance, bycatch, and population growth suggested that levels of bycatch were not sustainable in all Franciscana Management Areas (FMAs) in the early 2000s. These analyses led to the classification of the Franciscana as Vulnerable in the International Union for Conservation of Nature (IUCN) Red List (Zerbini et al. 2017). Abundance estimates obtained in the late 2000s showed a similar pattern, with bycatch levels ranging from 3% to 6% of the population size in all FMAs for which information is available. Other threats to the Franciscana include habitat degradation (Crespo 2018). A large proportion of the distribution range is subject to pollution from several sources, especially the agricultural use of land and heavy industries between São Paulo in Brazil, La Plata river, and Bahía Blanca estuary in Argentina. The coastal zone is also intensely used for boat traffic, tourism, and artisanal and industrial fishing operations (Crespo 2018).

In Patagonia, the biggest fishing effort since the 1980s was carried out with midwater and bottom trawl nets. There is no use of gillnets with the exception of Tierra del Fuego. The problem with trawls along the Patagonian coast is different in nature: in gillnets, cetaceans get trapped; in trawl nets, the animals enter in the net for taking fish or squid. For the first time incidental catch rates of marine mammals in trawl nets were estimated during the 1990s (Crespo et al. 1997). Working with fishing captains and officers allowed to estimate mortality rates. The species caught were South American sea lions, dusky dolphins, Commerson's dolphins, and common dolphins (Fig. 7). Other species were also recorded, i.e., South American fur seals and Peale's dolphins, but reported deaths for these species were infrequent.

Since the development of the hake *Merluccius hubbsi* trawling fishery in Patagonia, during the 1970s, sea lions have drowned in nets. The opportunistic behavior of taking advantage of new sources of food makes this species vulnerable. Sea lions interact with all types of fisheries, but are not killed in all of them (Crespo et al. 1994, 1997, 2007, 2012). They take the bait or fish caught in longlines and

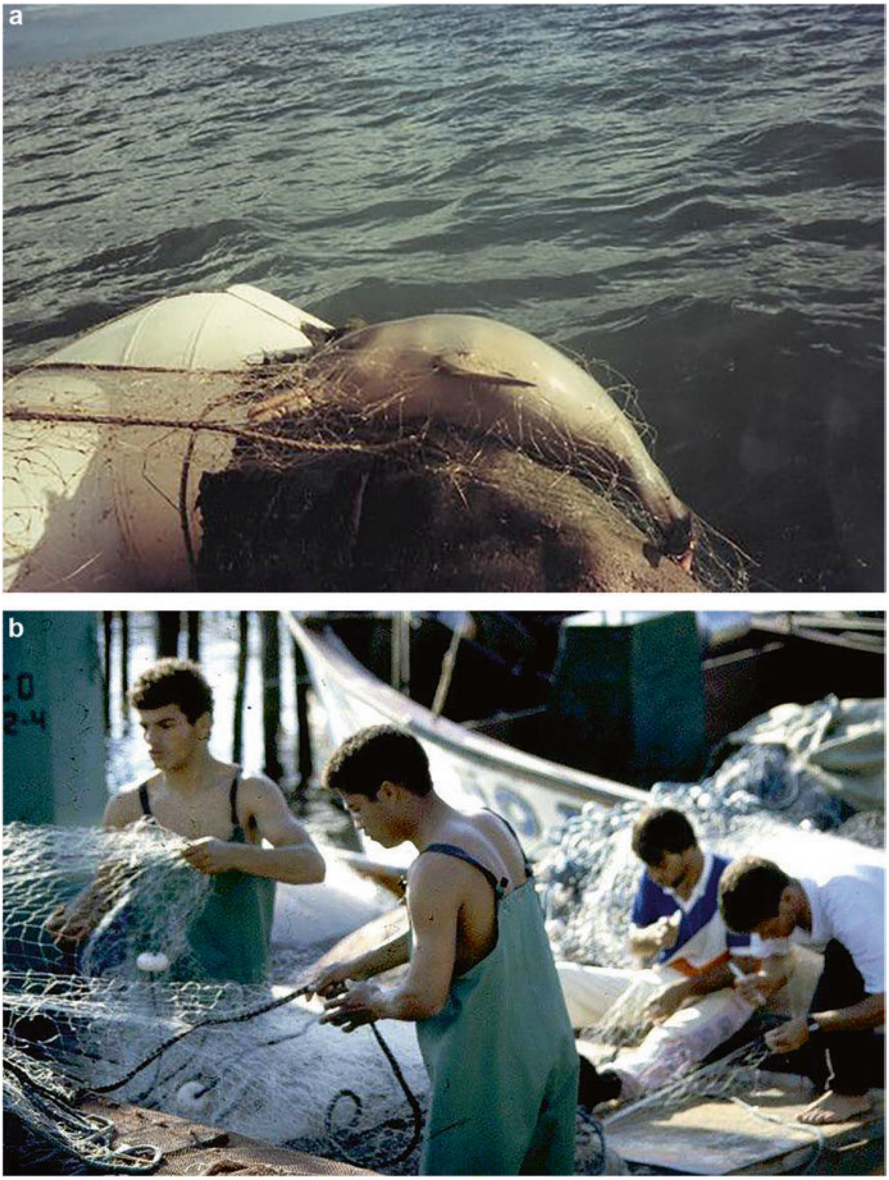

Fig. 6 (**a**) Franciscana dolphin entangled in coastal gillnets in Buenos Aires province (courtesy of Pablo Bordino), (**b**) fishermen in Rio Grande do Sul, Brazil (Courtesy of Eduardo R. Secchi)

gillnets, but are rarely caught in these gears. In Patagonian hake and shrimp *Pleoticus muelleri* trawls, mortality is roughly estimated between 1% and 2% of population size, which is today absorbed by a higher rate of increase, around 5.6%. Sea lion populations are still increasing and have not yet reached carrying capacity. Given

Fig. 7 Commerson's dolphins caught in mid-water trawls in Patagonian waters (photo Marine Mammal Laboratory CENPAT-CONICET)

the huge amount of biomass taken by the trawling and jigging fisheries, in which the main targets are also prey of sea lions, the carrying capacity in the next future may be very much lower than the original one. South American sea lions showed the lowest catch rates, but they were caught in seven of the nine types of the trawl fishery.

The mid-water trawl for shrimp showed the highest mortality rates for all the species. Between the 1970s and the 1990s, the negative effect on dusky dolphins was very severe given that the maturing females were the age and sex class mostly affected (Dans et al. 1997). In the following years, the fishing effort for shrimp and dolphin mortality decreased. Although mid-water trawls were forbidden for fishing shrimp in the mid-1990s, several experimental and commercial hauls were performed with this net to catch Argentine anchovies. Each time that one of these hauls was done, dusky and/or common dolphins were found entangled (Crespo et al. 2000). Eight events of dolphin mortality in mid-water fishing for anchovies were recorded during the 1990s in the Argentine sea. Some of these records simply noted that entanglements occurred and precise information was gathered only for three events. The mouth of the net was around 40 m high and 40 m wide. The catch rates estimated in those fishing operations reached almost nine individuals per day, per vessel, much higher than those calculated when fishing for shrimp. Several important features can be pointed out from the entanglement events in mid-water trawls: (1) the interaction was not passive, i.e., dolphins actively moved into the net; (2) entanglements seemed to be night-related; and (3) dolphin bycatches appeared to present a contagious distribution (Crespo et al. 2000)

Humans and Aquatic Mammals as Competitors

The direct exploitation of aquatic mammal resources for both primitive Paleolithic communities and modern societies can be considered as a predator-prey relationship from an ecological point of view. Since the mid-1960s, the exploitation of whales and other aquatic mammals has been questioned (Barstow 1990; Stroud 1996), and this has resulted in a stop of the direct exploitation of most of these populations. In the same period, however, a large increase in the extraction of biomass by the world's fisheries has resulted in other interactions between humans and aquatic mammals. A by-product of fisheries has been incidental mortality. However, in ecological terms, direct takes and incidental mortality in fishing gear are equivalent processes; animals die one way or the other. Species or areas may change but in essence show the same ecological events. At the same time these processes were going on, the fast development of technology increased the efficiency of fishers at a rate that the prey species cannot match (Crespo and Hall 2001). Because of this, management is needed to make a sustainable use of the resources based on science procedures that could allow for a cautionary management scheme.

The competition between aquatic mammals and humans has intensified to the point that today it is probably more significant than the direct exploitation of aquatic mammals (Crespo and Hall 2001). Competition and predation are key processes in the regulation of natural communities. In the particular case of interactions among top predators and fisheries, the competitive relationships have been a discussion point where culling proposals for the sake of fisheries are frequent topics (Yodzis 1994).

The concern often expressed over the quantities of fish consumed by seals, dolphins, and other marine mammals, and the possibility that they were affecting the size and availability of the fish stocks and thus the viability of fishing industries, led to demands made for culls to reduce the number of marine mammals. These thoughts stem from the belief that fewer marine mammals will consume less fish, which will leave more fish available for fisheries to catch, with resulting benefits for the fishing industry and the livelihood of fishers (Anonymous 1999). However, the scientific assessment of competitive interactions is not an easy task, considering the number of possible paths and the complexities of trophic links in the marine food web. Furthermore, long-term trends in the system can go in the opposite direction to short-term trends (Yodzis 1994). Experiences carried out in Canada, Great Britain, South Africa, and many other countries did not achieve the projected results in terms of a surplus of fish biomass after culling the respective populations of marine mammals (Bowen and Lidgard 2012).

In many cases, fisheries affect marine mammals by decreasing the abundance of their prey species. This problem has been well documented in Franciscanas. The interactions between the fishery operating in this region and the small cetaceans have been reviewed by Pinedo (1994) and Secchi et al. (1997). The principal prey of this coastal and river dolphin are the sciaenids, which have been severely depleted by coastal fisheries. Two studies conducted for the same area (Rio Grande do Sul) in 1982 and 1997 showed preliminary evidence of a shift in the diet of the Franciscana (Pinedo 1982; Bassoi 1997).

In Patagonia, the marine community is organized around the trophic system of three main target species: Argentine hake, Southern anchovy *Engraulis anchoita*, and Argentine shortfin squid *Illex argentinus* (Angelescu and Prenski 1987). At the same time, these species are key elements in the diet of most top predators and also are important fishery resources. Therefore, some of the basic conditions for competition are met if the species abundance decreases as a consequence of fishery extractions.

Koen Alonso (1999) studied the diet in several species of top predators including marine mammals and elasmobranchs. Figure 8 shows the proportion in the % index of relative importance (IRI%) of a few key and abundant prey species as part of the diet of South American sea lions, beaked skates *Zearaja flavirostris*, tope sharks *Galeorhinus galeus*, spiny dogfish *Squalus acanthias*, and dusky dolphins.

Sea lions show differences in diet with sex, and the skate and the dogfish show differences with sexual maturity using for feeding different parts of the water column (Koen Alonso 1999); therefore, they were treated as different trophic species. The bottom trawling fishery is included in Fig. 8. These and other top predators not considered here use the same prey species like hake and squids, as immature stages near the surface or mature stages close to the bottom.

At the end of the 1990s, it was estimated the food consumption by the South American sea lion population in northern and central Patagonia (Marine Mammal Laboratory unpub. information after Koen Alonso et al. 1999). The estimation was performed based on the individual daily intake and population size. In order to obtain mean daily intakes for males and females, the growth curves, age and sex

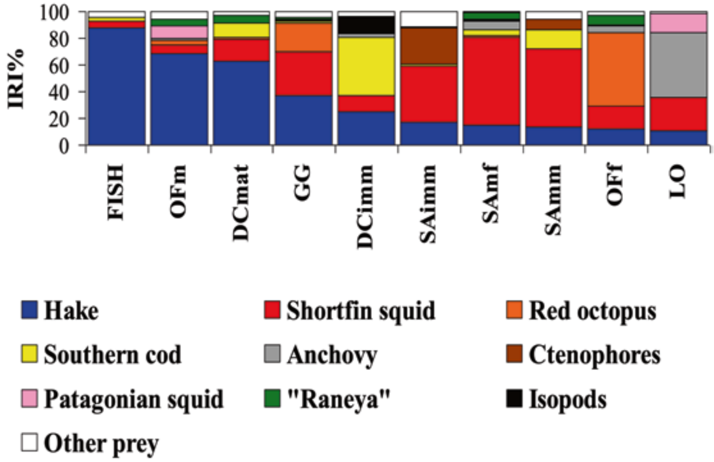

Fig. 8 Index of relative importance of prey of different top predators: OF *Otaria flavescens*, DC *Zearaja flavirostris*, GG *Galeorhinus galeus*, SA *Squalus acanthias*, LO *Lagenorhynchus obscurus*. m, male; f, female; im, immature; mat, mature (Marine Mammal Laboratory CENPAT-CONICET, unpubl.). FISH is trawling fishery

composition, and the rates of biomass ingestion equations for juveniles and adults of the Otariidae were used (Innes et al. 1987). The total population consumption was estimated on the basis of population size in 1996. The consumption by prey was obtained from the proportion in weight of each prey species in the diet and considering sex differences.

For the mid-1990s population of 67,800 sea lions, the total consumption was estimated in 148,000 metric tons, which include 72,000 tons for Argentine hake, 25,000 tons for the red octopus *Enteroctopus megalocyathus*, and 21,000 tons for the Argentine shortfin squid. Minor consumptions include 9,300 tons for the "raneya" *Raneya brasiliensis*, 4,300 tons for southern anchovy, 8,800 tons for the Patagonian squid *Doryteuthis gahi*, and 7,500 tons that correspond to 31 other prey species.

In the present day (late 2020s), the total number of sea lions in the Argentine sea, excluding the Malvinas islands, is around 130,000–135,000 individuals, twice of that in 1996 (Romero et al. 2017; Grandi et al. 2020). Therefore, the total consumption of prey may be twice as well. If the hake consumption by sea lions doubled, the take today is in the same order of magnitude of that of hake taken by the fishery, which reached around 270,000 tons in the last few years (Fig. 9). This means that this consumption should be considered in the management models for these species, at least for hake and shortfin squid.

The biomass extraction increased exponentially during the 1990s by means of an agreement with the European Union, reaching by 1997, 1.34 million tons considering all species caught. If the fishing discards are to be considered, the total extraction raises to 1.64 million tons (Fig. 9). At the late 1990s, the catches fell down, and after that they were sustained around 800,000 tons including 150,000 of fish

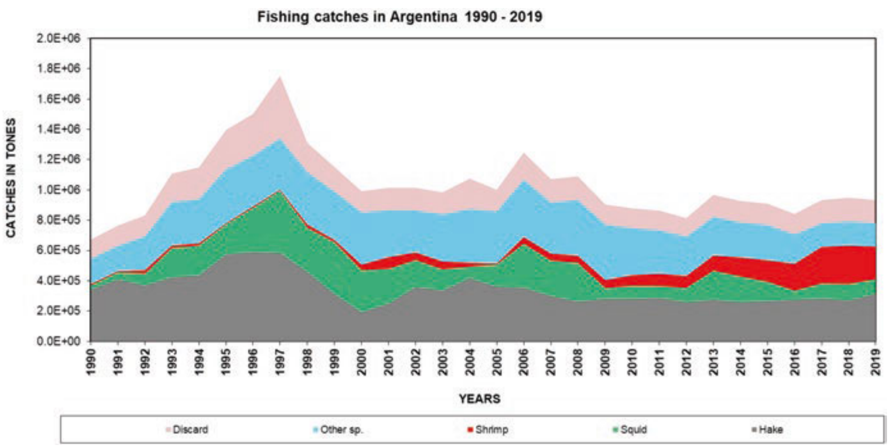

Fig. 9 Catches of target species of the trawling and jigging fisheries in Patagonia 1990–2018. (Data from Secretary of Fisheries and Aquaculture of Argentina and from the Marine Mammal Laboratory CENPAT-CONICET, unpubl.)

discards thrown back to the sea by the fishing vessels (Marine Mammal Laboratory unpub. information).

However, the structure of the food chain has changed; it is not the same as that 30 or 40 years ago when the trawling fishery grew exponentially. The relative abundance of the species in the community has changed as a consequence of the huge fishing extractions of biomass, but also by throwing thousands of tons of fish discards and wastes of the factory vessels back to sea and the mechanical action of the trawling nets at the bottom of the sea. This can be very easily seen in the changes in the diet of the beaked skate *Zearaja flavirostris*, which has been monitored for more than 30 years (Fig. 10). During the 1990s, the index of relative importance of common hake in the skate was around 50% of the biomass ingested. Thirty years after the IRI fell down to 10% with increases in other less nutritive species like the southern cod *Patagonotothen ramsayi* and hake heads and backbones found in the bottom of the sea thrown back to the sea by factory vessels (Koen Alonso 1999; Herrera 2011; Marine Mammal Laboratory unpub. information).

A recent analysis of Patagonian food webs across the past 7,000 years considered three top predators, sea lions, fur seals, and Magellanic penguins. Ancient food webs were shorter, more redundant, and overlapped more than current ones, both in northern-central and in southern Patagonia. This surprising result may be best explained by the huge impact of sealing on pinnipeds during the fur trade period, indicating that in modern food webs there has been a release from intraspecific competition and a shift toward larger and higher trophic-level prey (Saporiti et al. 2014). The three top predators overlapped more in the past. This, in turn, has led to longer and less overlapping food webs with fur seals and sea lions well below the original carrying capacity.

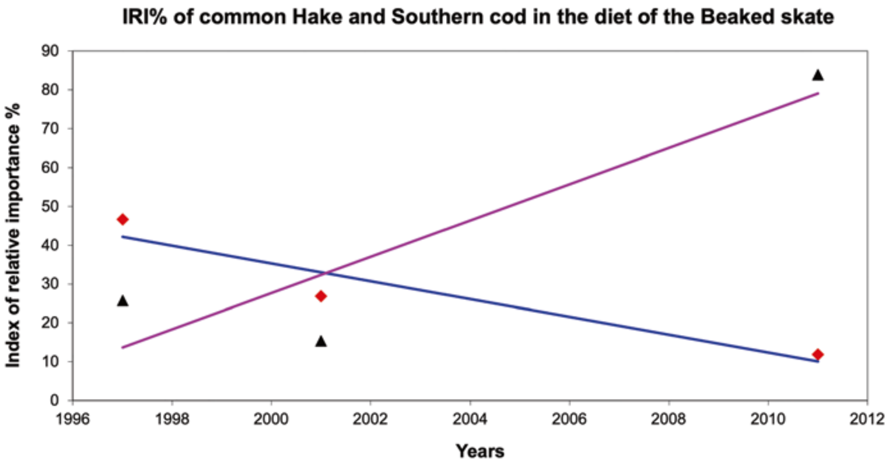

Fig. 10 Index of relative importance of two preys of the beaked skate in Patagonia (red diamond, common hake; black triangle, southern cod) (Marine Mammal Laboratory CENPAT-CONICET, unpubl.)

Economic Value of Marine Mammals: Substitution of Direct Takes by Ecotourism

With the moratorium on whale hunting and the changes in public attitude toward marine mammals, new economic activities have evolved in the last few decades, on the base of non-consumptive use of the species. Whale watching and ecotourism came to replace hunting and harvest and are now significant sources of benefits and employment in some areas of the world, mainly in western countries. However, uncontrolled whale watching and tourism can also have adverse impacts on the populations or the habitat. The IWC has started to consider this issue as another component of the management of the whale stocks (IWC 1997).

In Valdés peninsula whale watching started informally in 1973 and has been steadily increasing, based mainly on the observation of coastal wildlife. The southern right whale and the Magellanic penguins *Spheniscus magellanicus* are the main attractions, followed by the sea lions, the southern elephant seal, dusky, Commerson's, and common dolphins and other concentrations of nesting seabirds. It is clear, however, that the marine mammals of the area are the principal magnet for tourists. The number of tourists visiting Valdés peninsula has increased steadily in recent years, averaging 300,000 per year, while those watching whales is around one third (Anuario Estadístico de Turismo 2018–2019). The revenues in northern Patagonia to observe wildlife are close to U$S 100 million per year in direct benefits. It is impossible to predict today whether this industry will continue expanding for many years or if it will soon reach some kind of carrying capacity. By 2006, Argentina had the largest number of whale watchers in Latin America (Hoyt and Iñíguez 2008) and most of these came to Patagonia (Argentina).

In fact, very close to Valdés peninsula, the presence of whales in the northwest area of San Matías gulf within the San Antonio Bay Marine Protected Area (SABMPA) during winter and early spring has become frequent enough to set since 2012 an experimental program of whale-watching tourism. This planning was designed and implemented according to the current legal framework and enforced by the Environment and Sustainable Development Secretary (SAyDS) of the Río Negro province (Arias et al. 2018). Economic and educational benefits for the coastal communities are clearly positive aspects (Constantine and Baker 1997) and should provide adequate regulations in order to make the activity sustainable in the long term (Crespo and Hall 2001). However, in many places there is pressure from the private sector to open to tourism every attractive wildlife area along the coast and to allow the development of new activities, such as diving with dolphins, whales, and sea lions.

The other activities that produce significant economic benefits and employment in the region are fishing and oil exploitation. Both compete with ecotourism in the sense that, if it is well managed, ecotourism provides positive benefits to coastal communities while fisheries and oil activity may have negative ones. Overfishing of some of the target species, such as hake and squid, which are also important preys for many aquatic mammals and seabirds may produce decline of predators (Crespo et al. 1994, 1997; Koen Alonso et al. 1998, 2000), while oil exploitation and transport are important sources of pollution for wildlife and the marine environment at all levels (Geraci and St. Aubin 1990). Fisheries and oil activity as well as ecotourism provide employment for many people. Nevertheless, they have opposite actions one over the other. While the impacts of oil pollution on wildlife are sometimes very visible, the impacts of fishing (bycatch or unlimited biomass extraction) or tourism are less obvious to the public and are more difficult to trace to direct cause-effect mechanisms (Crespo and Hall 2001).

Marine Mammals and Climate Change

Aside from the problems for marine mammals that have been described in the previous sections, climate change has come to complicate the picture even more and make it less predictable. Marine mammals are usually considered as indicators of changes in their ocean environment. Despite being resilient animals, the rise of ocean temperature, acidification, and sea levels are just some consequences of climate change that may impact marine mammals in the near future, their food sources, and their habitats.

Although the effects of climate change on marine mammals are yet to be seen, it is clear that some species will be winners and others will be losers. In the case of the potential collapse of some populations, it may have therefore irreversible consequences for the ecosystem functioning and services (Albouy et al. 2020). Few cases of effects on populations have been documented in species living in SWA waters, mostly related to the Southern Ocean, which is connected to the SWA by water currents which, in turn, transport nutrients far north. Many species are connected to both areas by feeding and breeding, e.g., the southern right whale.

Klein et al. (2018) examined by means of ecosystem modeling how projected effects of ocean warming on the growth of Antarctic krill *Euphausia superba* might affect populations of krill and dependent predators (whales, penguins, seals, and fish) in the Scotia sea. The projected effects of ocean warming on krill biomass would be strongest in the northern Scotia sea, with a ≥40% decline in the mass of individual krill. These results may vary by location and species group. Klein et al. (2018) also stated that risk reductions at smaller spatial scales also differed from those at the regional level, which suggests that some predator populations may be more vulnerable than others to future changes in krill biomass. Their findings indicate the importance of identifying which species may be more vulnerable to negative effects of climate change and develop protection measures at different spatial scales, in order to avoid increasing risks with rising ocean temperatures.

Trathan et al. (2003) showed that the acoustic density of Antarctic krill at South Georgia is negatively related to temperature, with acoustic biomass reflecting variability in oceanographic conditions. They also showed that, over the past two decades, periods of high krill biomass have only occurred during anomalously cold periods and that the reduced levels of prey availability are linked with anomalously warm periods. If so, then low prey availability must affect the population processes of both gentoo penguins *Pygoscelis papua* and Antarctic fur seals. Long-term series of data showed that strong links exist between sea surface temperatures during the preceding winter period and fur seal breeding performance. For more than 20 years, positive anomalies in sea surface temperature in the tropical Pacific and at South Georgia explained significant nonlinear reductions in Antarctic fur seal pup production (Forcada et al. 2005). The same happened with gentoo penguins in years of lowest reproductive productivity for Antarctic fur seals (1990/1991, 1993/1994, 1997/1998, and 1999/2000) (Trathan et al. 2006).

The southern right whale is another krill eater that feeds in the waters around South Georgia and congregates to breed in the waters surrounding Valdés peninsula, Argentina (Leaper et al. 2006). Krill is the main prey at least for whales feeding to the south of 50° S as reported by Tormosov et al. (1998) based on stomachs of whales caught by the soviet fleet between 1951 and 1971. Whales taken north of 40° S were feeding on copepods. Between 40° and 50° S copepods dominated, but there were also euphausids in the sampled stomachs. Leaper et al. (2006) compared sea surface temperature (SST) time series from the SWA and the El Niño 4 region in the western Pacific to an index of annual calving success of the southern right whale breeding in Argentina. There they found a strong relationship between right whale calving output and SST anomalies at South Georgia in the autumn of the previous year and also with mean El Niño 4 SST anomalies delayed by 6 years. These results extend similar observations from other krill predators and show clear linkages between global climate signals and the biological processes affecting whale population dynamics. Seyboth et al. (2016) analyzed and concluded that the body condition and foraging success in the southern right whale might be affected by climatically driven change in the abundance of krill, the whales main prey on the feeding grounds. By means of cross-correlation analysis, they examined the response of the species to climate anomalies and krill densities and found that global climate indices influence southern right whale breeding success in southern Brazil by determining variation in krill availability for the species. Therefore, an increased frequency of years with reduced krill abundance, due to global warming, is likely to reduce the current rate of recovery of southern right whales from historical overexploitation.

Southern right whales were also subject to high mortality of calves in some particular years, namely, the seasons of 2008, 2009, and 2012. Many tissue samples were collected and analyzed, but no consistent lesions, pathologic processes, or elevated levels of algal biotoxins were identified that help explain these mortality events (Rowntree et al. 2013). Even that the mortality rate has been increasing since the early 1970s and it may be explained by a density dependence response (Crespo et al. 2019), the peaks of high mortality are not, and those particular years may be related to other temporal and spatial anomalies in the feeding areas that have not been detected yet.

With the exception of southern right whales, there is no evidence of climate change effects on marine mammal populations in Patagonian waters. In any case, these potential effects may be overlapped with other negative effects of anthropic origin such as fishery impact or pollution. What may then be expected? Marine mammals using beaches to rest or breed could be affected in habitat use if the sea level rises. This may be the case of the South American sea lion, which occupies more than 120 rookeries in the continental coast and islands. South American fur seals would be less affected since they live on rockier coasts. Furthermore, if the sea surface temperature rises, cryophilic species may also lose habitat.

It must be said that the recovery or loss of a given species sometimes does not depend on active policies. Many of them recovered only stopping the harvest or catches. Nevertheless, stopping the harvest or catches is not enough for a given species to recover, like in the northern right whale. The case of the vaquita *Phocoena sinus* is even worse; catches never stopped and still continued when the population was estimated to be under 20 individuals. In spite of the huge efforts and investment done in conservation, these species are going to be lost in the near future. The baiji *Lipotes vexillifer* was lost recently. Given the uncertainty of the future with climate change and all the variables playing a role is very little what humans may do to preserve the ecosystem in a reasonable shape.

What Should We Do with Marine Mammals?

There is a long debate around the utilization of marine mammals as a resource (Crespo and Hall 2001). The debate indeed revolves around two conflicting viewpoints. On the one hand, there are those who accept the utilization of marine mammals as a resource and defend their concerns on an adequate and cautious management, ensuring the sustainable use of populations in the long term. The IWC discussed policies on that basis (IWC 1994). On the other hand, there are those who do not accept the utilization of marine mammals as a resource, basing their views on a moral judgment that is strongly culture-dependent (Barstow 1990; Crespo and Hall 2001). In this case, there is no way to maintain an objective discussion. On the conservation side, there is also a need for objectivity in the sense that different situations or cases should be considered in the proper degree of importance. Otherwise, if every situation runs the same risk, for those officers that have to make management decisions, it is difficult to evaluate which alternative is the more important.

As can be seen, the interactions between aquatic mammals and humans are related, not only to ecology but also to ethics and economics. The interactions flow in many directions, and the solution for conservation and management of marine mammal populations lies in an integrated management in which all the stakeholders can define convenient courses of action that allow them to coexist. These parts should include the nations involved, fishermen, industry leaders, and environmentalists. Much of the success of conservation programs stems from the ability of the leaders of the different sectors to understand and communicate with each other and to find the common objectives that sometimes are lost in heated debates (Hall 1996, 1998).

Presently, most of the marine mammals, previously exploited or not, are recovering, some of them with high rates of increase. Sea lions increase at a rate of 5.6%, right whales at 2.2%, while from 2000 to 2007 they grew at 7%; fur seals are increasing at 8% (Crespo et al. 2015, 2019; Grandi et al. 2016). Sea lions and right whales are showing some evidence of density dependence. Sea lions seem to be reducing their bodies (Drago et al. 2010), and right whales are expanding from Valdés peninsula to deeper waters and San Matías gulf (Arias et al. 2018; Crespo et al. 2019). The only exception is the Franciscana for which the real effect of incidental mortality is unknown, whether it is sustainable or not. However, most of the species that were exploited in the past did not achieve yet the original population sizes. This is the case for the southern right whale, the sea lion, or the fur seal. For small cetaceans there is no previous information to which to refer original sizes or calculate rates of increase.

Possible Futures

The present chapter describes the history of the ecological relationships between a group of marine mammals and humans, the exploitation, and recovery of the most conspicuous top predators of the Southwestern Atlantic. It also attempts to explain the ecological mechanisms that allowed these species to recover. However, which are the potential scenarios that sea lions, fur seals, small cetaceans, and right whales may expect in an ecosystem in continuous change? None of them has reached yet a stable population size. However, they may and will reach one sooner or later and with high probability will be lower with regard to the original one. The huge amount of biomass extracted by the fishery will remain for decades. Therefore, in order to keep these and other top predator safe, there is a need of reaching an agreement of an equilibrium point in which the fishery catches may coexist with sustainable abundances of every one and all of the top predators in the ocean. This means to leave the necessary biomass to keep those populations safe. Nevertheless, the context of climate change in which these species are recovering may produce different results of those expected. Climate change is an uncertain threat to marine ecosystems and the services they provide and how it will affect the populations. Reducing fishing pressure is one option for mitigating the overall consequences for marine biota.

From an ecosystem point of view, the conservation and management of aquatic mammals require two very important things to consider: (a) mitigate the impacts of fishing gear and (b) deal with pollution and other forms of habitat degradation. It should also consider the coexistence of different forms of utilization *sensu* Hall (1996) following basic ecological principles avoiding the exploitation of some elements and protecting others and consider environmental variability in the short and long term and consider socioeconomic and cultural differences, including the development of an understanding and tolerance of those differences in all participants. Nowadays, management should be under international regulations, considering the different problems that need to be addressed. Global, regional, and local aspects of populations should be considered within a variety of alternative solutions, taking into account ecological, economic, "moral," cultural, and social variables (Hall 1996; Crespo and Hall 2001).

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