Geographic and temporal patterns of non-lethal attacks on humpback whales by killer whales in the eastern South Pacific and the Antarctic Peninsula

Killer whale attacks on humpbacks

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ABSTRACT: The role and impact of killer whales (*Orcinus orca*) as predators of baleen whales has been emphasized by studies of humpback whales (*Megaptera novaeangliae*). In this study, rake marks on the fluke were used as a proxy for predatory attacks in a sample of 2909 adults humpback whales and 133 calves from five breeding and two feeding locations in the eastern South Pacific and the Antarctic Peninsula. The goal of this study was to evaluate how often, at what age, where and when humpback whales were more susceptible to attacks. Overall, 11.5% of adults and 19.5% of calves had rake marks on their flukes. Significant differences were found in the prevalence of scars in calves when comparing breeding (9%) vs. feeding areas (34%) ($\chi^2 = 10.23$, $P < 0.01$). Multi-year sighting analysis of scar acquisition in 120 adults (82% site fidelity) and 37 calves at Magellan Strait showed no new marks after the initial sighting for the subsequent 15 years. This finding indicates that rake marks most probably were acquired when whales were calves, which support the belief that scar acquisition is a once in a lifetime event. The odds of having rake marks increased with time but with a significantly higher rate in calves ($\chi^2 = 5.04$, $P < 0.05$), which suggests an increase of predation pressure over time. Our results support the earlier hypothesis that killer whale attacks occur mostly on calves, near breeding sites and during the first migration to feeding areas.

KEY WORDS: Non-lethal attacks, eastern South Pacific, migration, humpback whale, killer whale, rake scars

INTRODUCTION

Killer whales (*Orcinus orca*) are apex predators of marine megafauna, including large marine mammals (Morisaka & Connor 2007). More than 20 species of cetaceans have been reported to be part of the killer whale's diet (Jefferson et al. 1991, Durban &

Pitman 2012, Pitman & Durban 2012). As regular prey of killer whales, cetaceans likely have developed behavioral strategies to reduce predation risk such as becoming silent, moving to shallow waters, hiding behind boats or escaping by fleeing (Jefferson et al. 1991). In an evolutionary context, the annual migration undertaken by most baleen whale species from high latitude summer grounds to low-latitude wintering grounds, where killer whales are less abundant, could be also a strategy to reduce predation risk (Corkeron & Connor 1999).

The ecological role of the killer whale as a predator of baleen whales has been debated for a long time as predatory attacks have rarely been observed (Clapham 2001, Connor & Corkeron 2001, Springer et al. 2003, Reeves et al. 2006). It seems that even those killer whales specialized on eating marine mammals do not regularly prey on baleen whales, as occurs with transient killer whales from the northeast Pacific that prey mainly on pinnipeds and small cetaceans and only occasionally on baleen whales (Ford et al. 2005). Another explanation for the scarcity of records of killer whales attacks on baleen whales could be a shift of killer whale prey preferences due to depletion of larger whale stocks caused by commercial whaling (e.g., Springer et al. 2003, DeMaster et al. 2006, Mizroch & Rice 2006, Trites et al. 2007, but also see Wade et al. 2007). However, recent records of attacks on humpback whales (*Megaptera novaeangliae*) observed off Western Australia (see Pitman et al. 2015) have contributed new insights about the importance of predation pressure by killer whales on baleen whales at breeding grounds. Either in a direct or opportunistic way, the predictability of baleen whales migration made them more susceptible to killer whales predation (Pitman et al., 2015).

Rake marks have been used as indirect evidence of predation attempts by killer whales on baleen whales, particularly in humpback whales (e.g. Mehta et al. 2007, Steiger et al. 2008). Scars can be observed on the flukes in this species when the whales raise the tail before a long dive. Although other less exposed parts of the body might also be scarred, they are less visible and harder to evaluate. Rake marks on humpback whale flukes and on other baleen whales caused by killer whale attacks have been confirmed in different parts of the world (Mehta et al. 2007, Steiger et al. 2008, Reinhart et al. 2013) and are considered to be evidence of unsuccessful or non-lethal attacks (Dolphin 1987, Clapham 2001, Naessig & Lanyon 2004, Mehta et al. 2007, Steiger et al. 2008, McCordic et al. 2014). It is not possible to establish the impact of killer whale predation on humpback whale populations based on such scars because scarred whales are survivors of unsuccessful attacks. However, the presence of killer whale rake marks on humpback whale flukes has been reported to be as high as 40% in some populations (Mehta et al. 2007, Steiger et al. 2008), indicating that important interactions occur between killer and humpback whales.

Humpback whale calves and yearlings seem to be more susceptible to killer whale attacks than larger, older cohorts (Reeves et al. 2006, Pitman et al. 2015). The likelihood of attack also seems to be higher during a whale's first migration from low latitude breeding grounds to high latitude feeding areas, suggesting that the marks are a once in a lifetime event resulting from an encounter with a killer whale (Clapham 1996, 2001, Mehta et al. 2007). However, this hypothesis is based on re-sightings of adult whales and not on multi-year sightings of individuals at different life history stages since were calves (e.g., Mehta et al. 2007, Steiger et al. 2008).

Most accounts of interactions between killer and humpback whales are from the North Atlantic or North Pacific (e.g., Mehta et al. 2007, Steiger et al. 2008, McCordic et al. 2014). Data for the Southern Hemisphere populations are scarce (e.g., Naessig &

Lanyon 2004, Pitman et al. 2015), particularly for the eastern South Pacific (ESP) (Flórez-González et al. 1994, Scheidat et al. 2000, Félix & Haase 2001, Mehta et al. 2007, Capella et al. 2014).

In this study we examined the incidence of rake marks on flukes of humpback whales belonging to Breeding Stock G, as referred to by the International Whaling Commission (IWC 2006). This population was estimated to be 6,504 (95% CI: 4270-9907) animals in 2006 (Félix et al. 2011). We considered the presence of rake marks to be indicative of non-lethal attacks and used the data to evaluate potential predation on humpback whales by killer whales. Our data come from several locations at feeding and breeding grounds along the ESP and the Antarctic Peninsula. Our goals were to determine how often, at what age, where and when humpback whales were more susceptible to killer whale attacks.

METHODS

Study area

The Breeding Stock G has the largest distribution of all humpback whale stocks in the world (Fig. 1). The breeding area extends from north of Peru (6ºS) to southern Costa Rica (12ºN) (Acevedo et al. 2007, Rasmussen et al. 2007, Pacheco et al. 2009) and the feeding area from the Antarctic Peninsula to sub-Antarctic waters at the Chilean fjords (Gibbons et al. 2003, Stevick et al. 2004). We included fluke data from animals photographed in five breeding and two feeding locations, collected by research groups led by the authors using different platforms, including research-dedicated surveys and opportunistic whale-watching vessels (see details in Félix and Haase 2011; Flórez-González 1991; Capella et al., 2012; Guzmán et al. 2015). Data from the Antarctic Peninsula were obtained from research vessels. Monitored sites at breeding grounds included Las Perlas Archipelago (8°22.414’N, 79°1.987’W) in Panama; Gorgona Island (2°58.244’N, 78°11.028’W) and Málaga Bay (3°56.274’N, 77°19.905’W) in Colombia; and Salinas (2°11.67’S, 80º58.3’W) and Machalilla (1°32.06’S, 80°49.9’W) in Ecuador. Feeding locations included the Magellan Strait (53°40.754’S, 72°14.354’W) off southern Chile and the Gerlache Strait (64°30’S, 62°20’W) in the western Antarctic Peninsula.

Assessment of rake marks

Individual whales used in this study were selected from institutional ID catalogs compiled in the period 1986–2015 (Table 1), based on the best-quality photographs with appropriate focus, definition, and perspective of the ventral surface of the flukes (Katona & Whitehead 1981). Rake marks were defined as a set of three or more parallel and equidistant linear scars on the ventral surface of the flukes (*sensu* Mehta et al. 2007). Analyzed images included only individuals for which images of both lobes of the tail were available to reduce bias by overestimating rates. Thereby, estimated rates should be considered as minimum values. Rake marks were solely attributed to encounters with killer whales and not to any other source (e.g., false killer whales, *Pseudorca crassidens*) based on the length, width and separation distance between the line scars (Mehta et al. 2007) as well as due to the lack of evidence of the presence of other potential predators of humpback whales in the region. Although, scars on flukes could also be produced when humpback whales interfered with attacks of killer whales (Pitman et al., 2007) there are not sufficient data to evaluate this issue.

Age/class categories

During fieldwork, individuals were assigned to one of three age classes based on the relative size of the animals: 1) adult: length > 12 m (visual estimation) or older than 4.5 years (when age was known); 2) calf: individuals < 9 months old and 8 m in length that maintained a constant/close relationship with an adult (presumably the mother); or 3) juvenile: whales of known age (1.5–4.5 years). The latter category was established with certainty only for the Magellan Strait due to availability of long-term individual data. In the case of data from breeding grounds, as not all research groups distinguished in the field the category juveniles, all non-calf individuals were considered as adults for the purpose of this study.

Intensity of rake marks

Rake marks were categorized according to the intensity of the injury as follows: 1) no rake marks on flukes (unmarked); 2) low: a single set of rake marks on one lobe or two sets of marks affecting < 10% of the lobe; 3) medium: at least one set of rake marks per lobe or more than two rake marks on one side covering up to 50% of the lobe; and 4) high: numerous marks covering more than half of the fluke and/or with missing sections on fluke tips or border (Fig. 2).

Prevalence of rake marks

Photographs of flukes of 3613 individuals (3443 adults and 170 calves) were examined, but only 2909 adults and 133 calves (a total of 3042) were selected and used for further analyses based on the defined quality criteria. All selected individuals identified from each site were included in the analyses based on the best photograph available for each individual. If an individual moved between sites, it was assigned to the location at which it was first sighted.

Acquisition rate of rake marks

The acquisition rate of rake marks as a function of sex and age was estimated by analyzing multi-year individual sighting data, which were only available for the Magellan Strait. The dataset contained 157 individuals, of which 94 (59.8%) were sexed using molecular techniques (Sabaj et al. 2004) or considered female when an adult was closely and consistently accompanied by a calf. Overall, 120 individuals were sighted for the first time as adults and 37 as calves during the period 1999–2015. A subset of 28 adult females, which calved from 1 to 5 offspring during this period, were used to determine whether the presence of a new calf influenced the acquisition of new fluke rake marks and to identify any possible bias related to breeding conditions. At this site individuals exhibited up to 80% interannual return (SD = 10, range 66.7–92.5%), with 75 whales returning annually for 5 or more years (Capella et al. 2012, Acevedo et al. 2014). This analysis was not possible for breeding sites due to the low interannual re-sighting rate, which usually was lower than 20% (Flórez-González 1991, Capella et al. 2008, Felix et al. 2011, Guzman et al. 2015).

Data modeling

A series of additive and interactive Generalized Linear Models (McCullagh & Nelder 1989) were used to tests whether the presence or absence of rakes (response variable) in humpback whales (n=3042) was a factor of the following three explanatory variables: ground (breeding, feeding), age (calf, adult-juvenile) and year (1986–2015). Five models were fitted and compared using the Akaike Information Criterion (AIC): one with a three-way interaction (rake~year*age*ground,family=binomial); two with a two-way interaction (rake~year*age, family=binomial) and (rakes~year*ground, family=binomial); one with ground as additive term (rake~year+ground, family=binomial); and one with age as interactive term and ground as additive (rake~year*age+ground, family=binomial). The models were fit with the function *glm* in R software environment version 3.2.2 (R Core Team 2015) with binomial family and logit link. Model significance was tested with Analysis of Variance and Chi-square tests, and predicted odds were estimated with the *predict* function.

Sighting Data – species distribution

Georeferenced sighting data on humpback and killer whales off the west coast of South America from the Regional System on Marine Biodiversity and Protected Areas of the Southeast Pacific (SIBIMAP), compiled by the Permanent Commission for the South Pacific (www.sibimap.net), were used for an additional analysis on the spatial distribution of both species. Data from SIBIMAP includes both published and unpublished information from oceanographic cruises, seismic prospection surveys and the Cetacean Sighting Network of the Chilean Navy. The dataset included 194 killer whale and 2214 humpback whale sighting records, containing a total of 949 and 5018 individuals, respectively. In addition, data from satellite transmissions on humpback whales were also included in this analysis (see Guzman and Félix, 2017). Distribution ranges were calculated for both species using the kernel density estimator to generate surface values indicating higher or lower utilization of the space with the Spatial Analyst tool in ArcGis, Version 10.2.2.

RESULTS

Rake mark prevalence

Rake marks were found in 361 of the 3042 individuals assessed (11.86%) (Table 1). The sample size was highly variable between locations and between feeding and breeding areas. The largest photograph datasets were from Ecuador (60.5%) and Colombia (25.7%). The feeding grounds photograph dataset represented 9.2% of the total sample.

Overall rake prevalence rates of 0.115 for adult whales (335 of 2909) and 0.195 for calves (26 of 133) were found (Table 1). The prevalence of rake marks on flukes ranged from 0.088 to 0.159 in adults and from 0.065 to 0.339 in calves (Table 1). The proportion of rake marks in adults from breeding (mean = 0.11, SD = 0.02) and feeding areas (mean = 0.14, SD = 0.03) was not significantly different ($X^2 = 2.02$, $P > 0.05$), but the proportion of rake marks in calves between breeding and feeding areas (mean = 0.11

vs. 0.34, respectively) was highly significant ($X^2 = 10.23$, $P < 0.01$), representing a 3.1 time increase. No data on calves from the Antarctic were available for this comparison.

The intensity of rake marks on flukes was assessed in adult whales for each site except Gerlache Strait at Antarctic Peninsula (because of its small sample size, n = 8). The most frequent category was unmarked, with an average of 87.7% (SD = 2.8, range 84.1 – 91.2, n = 2513) (Fig. 3). Regarding marked whales, the most frequent category was low intensity, with an average of 57.4% (SD = 5.8, n = 171) of all scarred whales (ranging from 47.8% in Salinas-Machalilla, to 61.5% in Malaga Bay. The medium intensity category averaged 27.8% (SD = 6.8, n = 79) of scarred whales (ranging from 21.5% in Salinas-Machalilla to 38.5% in Malaga Bay). The high intensity category averaged 14.8% (SD = 11.1, n=77) of scarred whales (ranging from 0% in Malaga Bay to 30.7% in Salinas-Machalilla). This last category was the most variable among the three categories and was significantly higher in Salinas-Machalilla and significantly lower in Malaga Bay ($\chi^2_8 = 28.43$, $P < 0.01$).

Acquisition of rake marks

No acquisition of rakes in unmarked individuals nor new rakes in individuals first time identified with rake marks as adults was found at breeding areas throughout the study period (n = 391). Multi-year sighting data from the Magellan Strait dataset also revealed no new marks in subsequent observations of animals first observed with scars (n = 32; 22 adults and 10 calves) or first observed unmarked (n = 108; 81 adults and 27 calves). None of 27 unmarked calves with return histories to Magellan Strait (average 5 different years, SD = 3, range 2 – 11) acquired new rake marks either as juveniles or adults (maximum 11.5 years old) (see Table 2).

Of 25 whales with rake marks at the Magellan Strait, 7 were males (28%), 8 were females (32 %), and 10 were of undetermined sex (40%). Of the 132 whales without rake marks, 39 were males (29.5%), 44 were females (33.3%), and 49 were of undetermined sex (37.1%). No sex bias was found regarding rake marks, as the proportion between sexes was not significantly different ($\chi^2 = 0.144$, $P > 0.05$). The acquisition of new rake marks in either unmarked or marked adult females that calved during the study period at Magellan Strait (1999–2015) was assessed. Mothers with initial fluke rake marks (n = 5) produced 16 calves: 5 (31%) acquired rake marks, 6 (38%) did not, and presences/absence could not be determined in the other 5 calves (31%) as calves did not expose their flukes. Initial unmarked mothers (n = 29) produced 64 calves: 14 (22%) acquired rake marks, 31 (48%) did not, and presences/absence could not be determined in the other 19 (30%). No significant differences were found in the proportion of marked, unmarked, and undetermined calves between marked and unmarked mothers ($\chi^2 = 0.84$, $P > 0.05$). In addition, mothers that experienced a killer whale attack prior to calving had a higher calving rate than unmarked mothers (3.2 and 2.2 calves per female, respectively).

Long-term dynamics

The model with the lower AIC value showing the interaction (age x location) of the four competing models was used to examine the presence or absence of rake marks (Table 3). The results of the generalized linear model of the complete three-way interaction between whale age, site, and year was not significant ($\chi^2 = 1.22$ $P > 0.05$). However, when the model was reduced to the interaction between age and year (and ground as an additive term), a significant relationship was found ($\chi^2 = 5.04$, $P < 0.05$).

Thus, there was a different relationship between the presence of rake marks and year than between calf and adult whales and ground (Fig. 4). The odds of having rake marks increased with time from 1986 to 2015 and this increase was remarkable higher in calves in both breeding and feeding grounds.

Sighting distribution analysis

Available information from the SIBIMAP dataset on humpback and killer whales show that both species are found along the ESP region, including breeding, feeding and migratory routes for humpback whales (Fig. 1). Distribution overlapping includes both coastal and offshore waters, but is particularly more pronounced at breeding grounds around the Galapagos Archipelago, the southern Ecuador, off Peru, as well as along most of the coast of Chile. Humpback whale dataset at breeding grounds is likely biased towards the coast because research effort was concentrated in coastal areas. On the other hand, most data from killer whales are from oceanographic cruises and therefore less unbiased.

DISCUSSION

This is the first study on non-lethal predatory encounters between humpback and killer whales inhabiting the ESP and the Antarctic Peninsula using rake marks as indirect evidence of predation. We confirm that in the southeast Pacific humpback whale population predation by killer whales mainly occurs at breeding grounds or during the first migration to feeding grounds, in similar way as proposed for other populations (Clapham 1996, 2001, Mehta et al. 2007). This belief is supported by detected differences in the proportion of rake marks in calves between breeding and feeding sites in the ESP (9% at breeding grounds and 34% at the Magellan Strait feeding site) and the lack of acquisition of new marks after the first year of life. Additionally, despite numerous sightings of killer whales (n = 63) during the summers of 2004 to 2012 in the Magellan Strait, no attacks on humpback whales were observed while feeding on sea lions, fish and sea birds were recorded (Capella et al. 2014). Killer whale chasing behavior on sei whales (*Balaenoptera borealis*) (but not on humpbacks) was once observed 1000 km northward from the Magellan Strait at North Patagonian fjords, a secondary humpback feeding ground (Hucke-Gaete et al. 2013) and also in the Beagle channel, 200 km south of the Magellan Strait (RNP Goodall com pers). The diet of killer whales in northern fjords is also composed mainly by sea lions, fur seals and sea birds (Haussermann et al. 2013).

We consider our sample size to be representative of Breeding Stock G at two feeding locations (the Magellan Strait and Gerlache Strait) and five breeding locations along three countries (Panama, Colombia, and Ecuador) (Stevick et al. 2004, Acevedo et al. 2007, Guzman et al. 2015). The conclusions of this study benefit from the analysis of large datasets (2909 adult and 133 calves selected) that encompass a large proportion of individuals belonging to Breeding Stock G (see Félix et al. 2011).

Overall, rake marks on adult humpback whales in both feeding and breeding areas (11.5%, range 8.8–15.9%) was in the range of that reported for other populations elsewhere (globally 1.2–40.1, Mehta et al. 2007; 5–31% for the North Pacific, Steiger et al. 2008; 2.7–17.4% for the North Atlantic, McCordic et al. 2014; 15.9–31.3% off western and eastern Australia, Tonga, and New Caledonia, Mehta et al. 2007; Naessig & Lanyon 2004). Our results also are consistent with those of Steiger et al. (2008)

regarding the lack of differences in the proportion of scarring in adults between breeding and feeding areas. However, the data from the Antarctic Peninsula contrast with those of Mehta et al. (2007), for the same area, who estimated a rake marks prevalence of 1.2% based on 164 individuals assumed to be adults. This value seems to be underestimated compared with our findings from the Gerlache Strait, Antarctic Peninsula (11.6%), and from the Magellan Strait (15.9%), a secondary feeding location in the South of Chile.

We found that both male and female were scarred to comparable extents in the Magellan Strait, where almost equal overall sex ratio exists (Capella et al. 2012; Acevedo et al. 2014), something that is expected at feeding grounds (Clapham et al. 1995). The absence of additional scars in multi-year sighting adults and in multi-calving females, even those with already scarred calves, could be explained by killer whales avoiding the tail of adults and mothers during attacks, either by attacking other body parts as reported by Flórez-González et al. (1994) and Pitman et al. (2015) or by just focusing on the calf. Anti-predator behaviors by humpback whales involve the presence of escorts to defend the mother-calf pair as well as approaching shallow areas where killer whales would have less maneuverability (Jefferson et al, 1991; Pitman et al. 2015). Humpback whales have been reported interfering attacks by mammal-eating killer whales not only on conspecific mother/calf pairs but also on other aquatic species (Pitman et al., 2017). Preferences on nearshore waters, especially for mother-calf pairs (Erts & Rosenbaum 2003, Felix & Botero 2011, Craig et al. 2014) has been mentioned as a strategy for protection from killer whale predation (Pitman et al. 2015), which would extend during the migration. Female humpback whales and their calves take a coastal migratory route than other adults towards feeding grounds, which has been shown with satellite tracking data in the ESP (Félix & Guzman, 2014), and also observed along eastern Australia (Franklin et al. 2017). Additionally, our data from the Magellan Strait indicated that females that were attacked as calves (scarred whales that survived the attack) arrived to feeding area with higher number of calves that survived the first migration (3.2 per female) than non-attacked (non-scarred) females (2.2). However, no data is available about calf mortality during breeding season and migration. Even though, this apparent higher survival of calves at the first migration suggests that females attacked when young may develop anti-predator tactics to avoid killer whale predation on their own calves as a result of her individual experience.

The spatiotemporal patterns of attacks of killer whales seem to be dependent of species and geographic location. Our results for ESP humpback whales, therefore, are not necessarily comparable with information for other baleen whales. For example, incidence of attacks on Bowhead whales is higher for old adults than for sub-adults and juveniles, as rake marks are cumulative in time for each individual (Reinhart et al. 2013).

On the other hand, the hypothesis of predation risk reduction as a major selective advantage for baleen whales to explain their annual migration towards lower latitudes to breed (Corkeron & Connor 1999, Connor & Corkeron 2001) is not supported by our study (see also Steiger et al. 2008) at least for humpback whales. The fact that other baleen species such as the bowhead whales (*Balaena mysticetus*) and the pygmy right whale (*Caperea marginata*), do not migrate for breeding in the tropics also suggest that several factors are associated to whale migration. The result of this study regarding the timing of scar acquisition, based on data on rake marks in calves and adults/juveniles, and multi-year sighting history (including the transition from calf to adult) from the

Magellan Strait, strongly support the hypothesis that killer whale attacks occur specifically on calves (Clapham 1996, 2001). Available data on the distribution of both humpback whales and killer whales along the ESP shows a clear overlap and supports the hypothesis that predation occurs either at the breeding site or during the migration. Similar predation patterns by transient killer whales on gray whales' calves (*Eschrichtius robustus*) during the migration to feeding grounds have also been reported along the northeast Pacific (Barrett-Lennard et al. 2011, Pittman et al. 2014).

Modelling results show a significant higher increase in odds of having rake marks in calves during the study period (1985 to 2015) at both breeding and feeding grounds respect to adults. This may be because killer whale populations preying on baleen whales increased as baleen whale populations rebounded after the whaling moratorium or because there was a shift (return) in killer whale predation on baleen whales because of baleen whale increased availability. Killer whale sightings seem to have increased in tropical areas from Costa Rica to Peru. For example, there were 50 sightings near Machalilla, Ecuador between 1997 and 2004, with 8 cases charging and attacking humpbacks (Castro et al. 2005), and 5 sightings between 2013 and 2016, resulting in 3 calves killed (C Castro pers. comm.). At least 33 sightings were reported during several pelagic surveys in Peru (Garcia-Godos 2004, summarized in Guerrero-Ruiz et al. 2005), and there were 5 sightings between 2011 and 2017 in Panama (HM Guzman unpublished data). Consequently, an increase in attacks can be expected (*sensu* Pitman et al. 2017). Although in some cases increased killer whale sightings may be the result of increased effort, in others such as in Ecuador the effort has been more uniform, and therefore the trend seems real.

Almost 3/4 of flukes with rake marks in ESP humpback whales (11.86% of the total dataset) had low to moderate scarring. Previous studies have reported that two-thirds or more of the humpback whales studied had rake marks at the mid-to-moderate scarring level, and less than 10% had severe scarring (Naessig & Lanyon 2004, Mehta et al. 2007, Steiger et al. 2008). We interpret these results as follows: 1) attacks resulting in severe damage (as defined here) are rare, and/or (2) attacks resulting in severe damage are often lethal. The significantly higher proportion of whales with severe scarring observed in Salinas-Machalilla (Ecuador) with respect to other breeding locations may be related to different predation pressure at the sampled locations and the fact that this population shows a high level of stratification at breeding grounds (Guzman & Félix 2017). Further research of killer whale distribution and movements are required in this part of the ESP.

CONCLUSIONS

We set out to determine how often, at what age, where and when humpback whales were most susceptible to attack and/or acquisition of rake scars from killer whales in the ESP. We conclude the following:

1. The frequency of rake marks on flukes of adult humpbacks in feeding and breeding sites in the ESP and the Antarctic was like those reported elsewhere.
2. The incidence of rake marks on calves was significantly higher at feeding than at breeding grounds. Therefore, calves acquired rake marks at breeding sites and during the first migration to feeding areas.

3. Multi-year sightings of 103 adults and 37 calves from the Magellan Strait revealed no new marks on flukes after the initial sighting. No whales acquired rake marks either as juveniles or adults.
4. Calf presence did not cause the acquisition of new rake marks in either unmarked or marked mothers. None of the mothers gained scars or new marks during calving. Calves from both types of mothers were comparably susceptible to acquiring rake marks.
5. An attack with non-lethal consequence on a female calf seemed to have a positive impact *a posteriori* increasing their own offspring's survival.
6. Calves showed a significant increase in the probability of having rake marks along the study period respect to adults, which suggests an increase of predation pressure over the time.

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Table 1. Percentage of rake marks in the flukes of 2909 adult and 133 calf humpbacks whales photo quality-selected from the eastern South Pacific and the Antarctic Peninsula. Total analyzed = includes all individuals initially screened from catalogs, including discarded individuals with one lobe or limited definition of the fluke's picture.

	Sampling period	Total analyzed		Total selected		Rakes in Adults		Rakes in Calves	
Location		Adult	Calf	Adult	Calf	N	Rate	N	Rate
Las Perlas (Panama)	2003–2009	133	9	128	8	18	0.140	1	0.125
Malaga Bay (Colombia)	1993–2001	170	63	147	46	13	0.088	3	0.065
Gorgona Is. (Colombia)	1986–2004	762	20	581	8	66	0.113	1	0.125
Salinas-Machalilla (Ecuador)	1991–2013	2,151	15	1,827	15	205	0.112	2	0.133
Magellan Strait (Chile)	1999–2015	158	63	157	56	25	0.159	19	0.339
Gerlache Strait (Antarctic)	2012-2015	69	0	69	0	8	0.116	*	*
Total	1986–2015	3,443	170	2,909	133	335	0.115	26	0.195

*Values not available.

Table 2. Multi-year sighting history of 37 returned calves identified by fluke to the Magellan Strait feeding area. Empty space indicates no available data. A= Flukes without rake marks. P= flukes with rake marks. NP= Flukes without new rake marks. M= Male. F= Female. UN= Sex undetermined.

		Age											
SEX	**ID**	**< 1**	**1.5**	**2.5**	**3.5**	**4.5**	**5.5**	**6.5**	**7.5**	**8.5**	**9.5**	**10.5**	**11.5**
M	59	A		A	A					A			A
F	65	A	A	A		A	A	A	A	A	A	A	A
F	78	A	A	A	A	A	A	A	A	A	A	A	
F	79	A	A										
F	80	P		NP	NP	NP	NP	NP	NP	NP	NP		
F	91	A	A	A	A	A	A	A	A	A	A	A	
M	97	A	A	A	A	A	A	A	A	A	A		
F	99	P			NP	NP							
F	101	P	NP		NP			NP					
UN	103	P		NP									
F	105	A		A	A	A	A	A	A	A	A		
F	109	A			A	A	A		A	A	A	A	
F	115	A	A	A	A	A	A	A	A				
UN	117	A			A	A	A						
UN	118	A	A		A								
UN	119	P			NP	NP	NP	NP	NP	NP	NP		
UN	120	A		A		A	A	A	A				
UN	121	A		A									
UN	122	A	A	A	A	A	A	A	A				
UN	127	A	A			A	A						
UN	128	A				A	A						
UN	129	P			NP			NP					
UN	130	A	A	A	A								
UN	134	A		A									
M	141	A					A						
UN	142	A			A	A	A	A					
UN	143	A					A			A			
UN	144	A						A					
UN	145	A		A	A	A	A						
UN	146	A						A	A				
UN	152	A		A	A	A							
UN	153	P			NP	NP							
UN	156	P			NP	NP							
UN	157	A				A							
UN	158	A			A								
UN	163	P			NP								
UN	165	P		NP									

Table 3. Results of AIC analysis for the four competing models used to examine the presence or absence (response variable) of rake marks on Humpback Whale flukes.

Explanatory variable	p-value	AIC
Location (breeding or feeding ground)	0.0007 ***	2208.8
Age (calf or adult/Juvenile)	0.00919 **	2213.4
Age + Location	Age: 0.072390 Location: 0.005118**	2207.6
Age *x* Location	Interaction: 0.007800**	2202.5

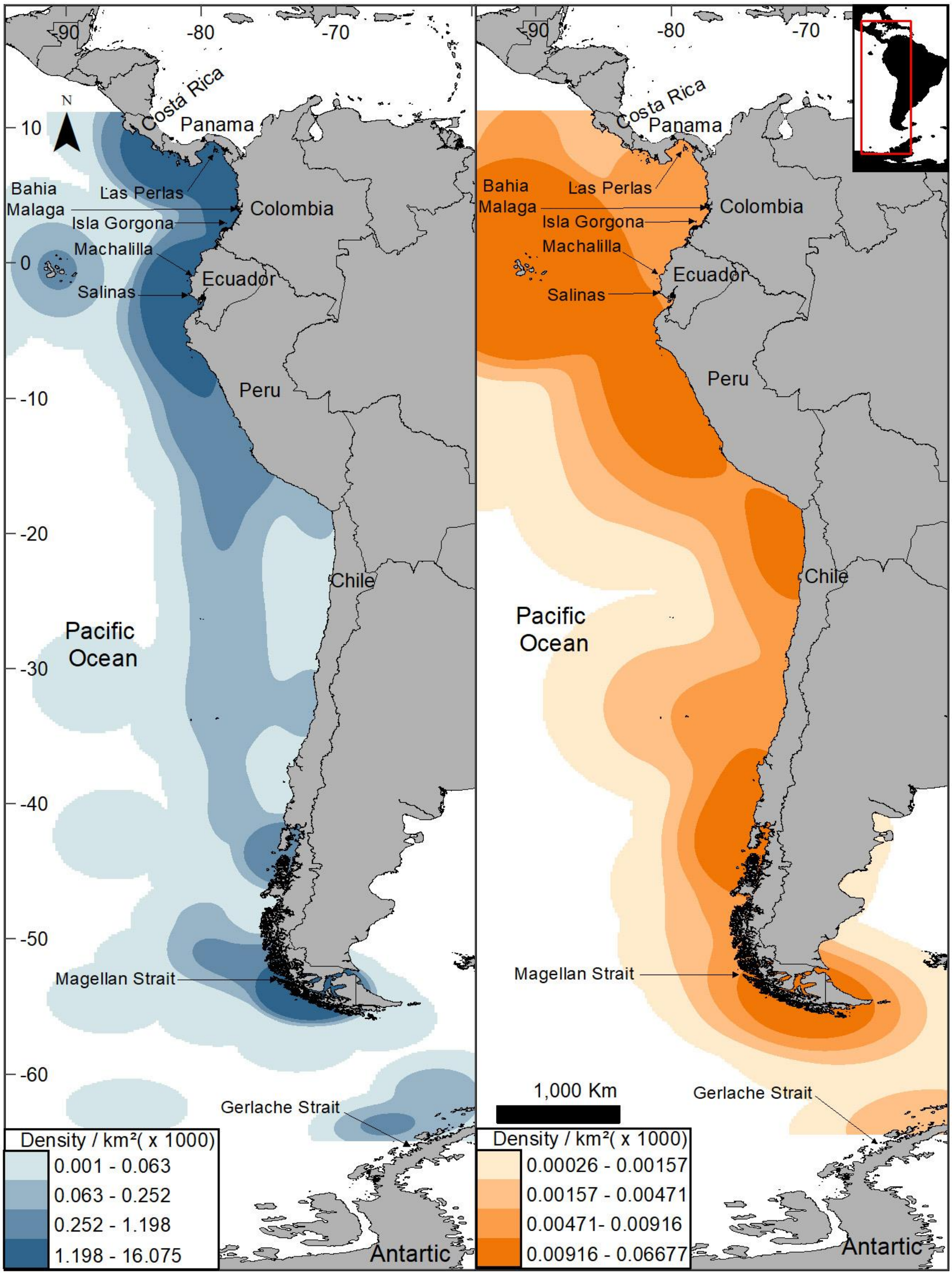

Fig. 1. Map of the eastern South Pacific showing the location of breeding and feeding (black arrows with site names) areas evaluated in this study as well as the density kernel distribution of satellite tracked from Guzman & Felix (2017). Reported sightings data of humpback whales (left map) and killer whales (right map) along the region from SIBIMAP.

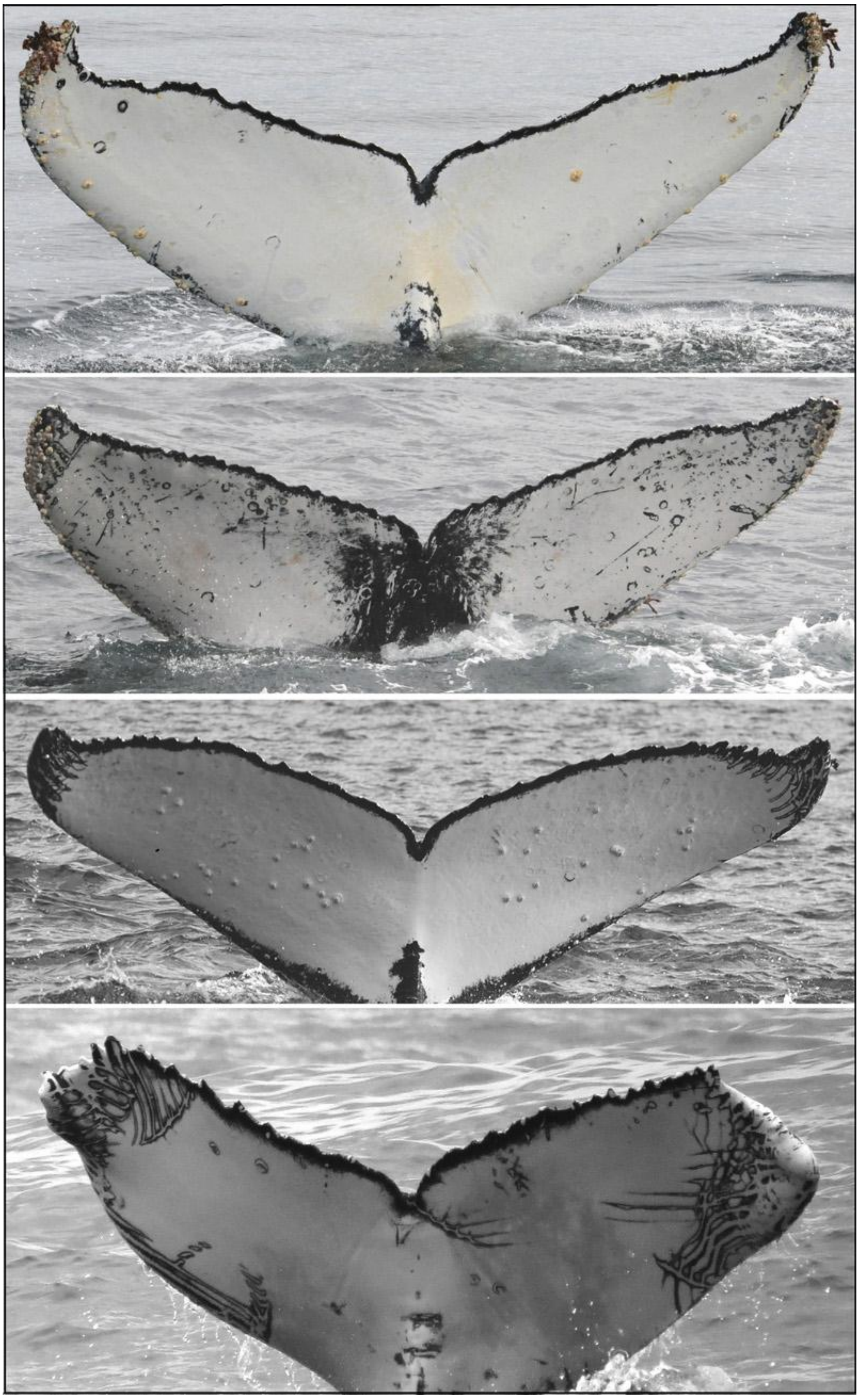

Fig. 2. Humpback whale flukes unmarked and with rake marks of different intensity. From top to bottom: unmarked, low, medium and high intensity.

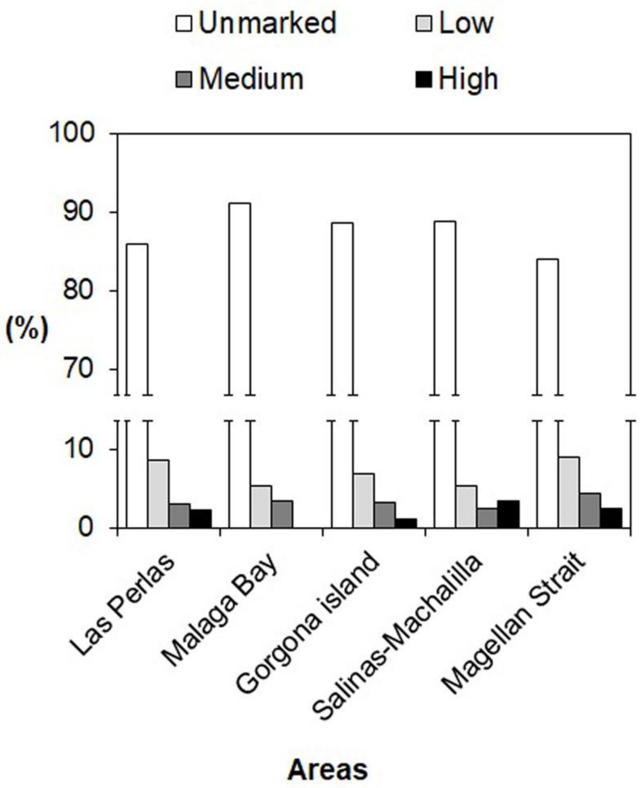

Fig. 3. Percentage of four level intensity of rake marks (as defined in text) on humpback whale flukes of adult and juveniles from whales inhabiting the eastern South Pacific (n = 327).

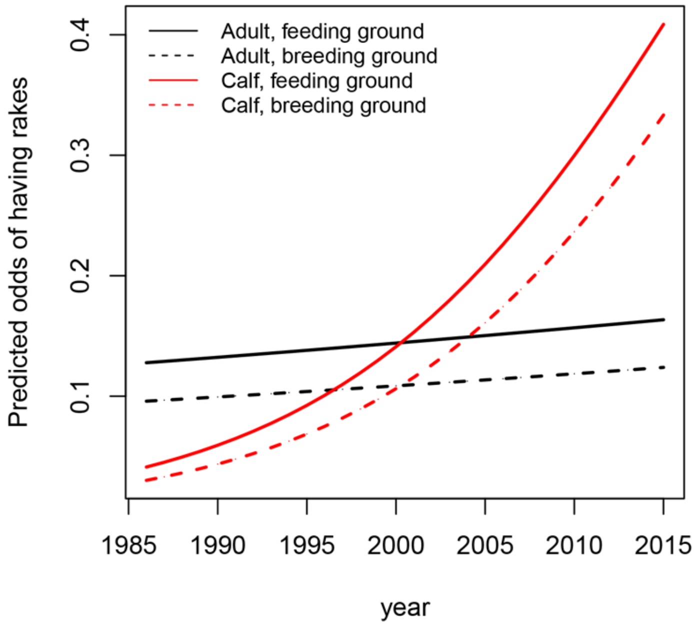

Fig. 4. The odds of having rake marks with time (years) for calves and adults at both breeding (Panama, Colombia and Ecuador) and feeding grounds (eastern South Pacific and Antarctic Peninsula). Data included the period 1986–2015.