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Gretchen H. Steiger
Cascadia Research Collective, 218% West Fourth Avenue, Olympia, Washington 98501, USA

John Calambokidis
Cascadia Research Collective, Olympia, Washington

Janice M. Straley
University of Alaska Southeast

Louis M. Herman
University of Hawaii and the Dolphin Institute

Salvatore Cerchio
OSS Landing Marine Laboratories

See next page for additional authors

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Authors

Gretchen H. Steiger, John Calambokidis, Janice M. Straley, Louis M. Herman, Salvatore Cerchio, Dan R. Salden, Jorge Urban-R., Jeff K. Jacobsen, Olga von Ziegesar, Kenneth C. Balcomb, Christine M. Gabriele, Marilyn E. Dahlheim, Senzo Uchida, John K. B. Ford, Paloma Ladron de Guevara-P., Manami Yamaguchi, and Jay Barlow

Geographic variation in killer whale attacks on humpback whales in the North Pacific: implications for predation pressure

Gretchen H. Steiger[1,*], John Calambokidis[1], Janice M. Straley[2], Louis M. Herman[3], Salvatore Cerchio[4,17], Dan R. Salden[5], Jorge Urbán-R.[6], Jeff K. Jacobsen[7], Olga von Ziegesar[8,18], Kenneth C. Balcomb[9], Christine M. Gabriele[10], Marilyn E. Dahlheim[11], Senzo Uchida[12], John K. B. Ford[13], Paloma Ladrón de Guevara-P.[14,19], Manami Yamaguchi[15], Jay Barlow[16]

[1]Cascadia Research Collective, 218½ West Fourth Avenue, Olympia, Washington 98501, USA
[2]University of Alaska Southeast, 1332 Seward Avenue, Sitka, Alaska 99835, USA
[3]Kewalo Basin Marine Mammal Laboratory, University of Hawaii and the Dolphin Institute, 420 Ward Avenue, Honolulu, Hawaii 96814, USA
[4]Moss Landing Marine Laboratories, PO Box 450, Moss Landing, California 95039, USA
[5]Hawaii Whale Research Foundation, 52 Cheshire Drive, Maryville, Illinois 62026, USA
[6]Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, Ap. Post 19-B, La Paz, BCS 23081, Mexico
[7]Humboldt State University, Department of Biological Sciences, Arcata, California 95521, USA
[8]North Gulf Oceanic Society, PO Box 15244, Homer, Alaska 99603, USA
[9]Center for Whale Research, 1359 Smuggler's Cove Road, Friday Harbor, Washington 98250, USA
[10]Glacier Bay National Park, PO Box 140, Gustavus, Alaska 99826, USA
[11]National Marine Mammal Laboratory, NOAA, 7600 Sand Point Way NE, Seattle, Washington 98115, USA
[12]Okinawa Churaumi Aquarium, Motobu-cho, Okinawa-ken 905-0206, Japan
[13]Pacific Biological Station, Nanaimo, British Columbia V9T 6N7, Canada
[14]Facultad de Ciencias, Universidad Nacional Autónoma de México, Ap. Post 70-572, México DF 04510, Mexico
[15]Ogasawara Marine Center, Byobudani, Chichijima, Ogasawara-mura, Tokyo 100-2101, Japan
[16]Southwest Fisheries Science Center, 8604 La Jolla Shores Dr., La Jolla, California 92037, USA

[17]Present address: Wildlife Conservation Society, American Museum of Natural History, Central Park West, New York, New York 10024, USA

[18]Present address: Eye of the Whale, PO Box 15191, Homer, Alaska 99603, USA

[19]Present address: Instituto Nacional de Ecología c/o CICESE Km 107 Carr. Tijuana-Ensenada, Ensenada, BC 22860, Mexico

ABSTRACT: We examined the incidence of rake mark scars from killer whales *Orcinus orca* on the flukes of humpback whales *Megaptera novaeangliae* throughout the North Pacific to assess geographic variation in predation pressure. We used 3650 identification photographs from 16 wintering or feeding areas collected during 1990 to 1993 to determine conservative estimates in the percentage of whales with rake mark scarring. Dramatic differences were seen in the incidence of rake marks among regions, with highest rates on wintering grounds off Mexico (26 vs. 14% at others) and feeding areas off California (20 vs. 6% at others), 2 areas between which humpback whales migrate. Although attacks are rarely witnessed, the prevalence of scars demonstrates that a substantial portion of animals are attacked, particularly those that migrate between California and Mexico. Our data also suggest that most attacks occur at or near the wintering grounds in the eastern North Pacific. The prevalence of attacks indicates that killer whale predation has the potential to be a major cause of mortality and a driving force in migratory behavior; however, the location of the attacks is inconsistent with the hypothesis that animals migrate to tropical waters to avoid predation. Our conclusion is that, at least in recent decades, attacks are made primarily on calves at the wintering grounds; this contradicts the hypothesis that killer whales historically preyed heavily on large whales in high-latitude feeding areas in the North Pacific.

KEY WORDS: Killer whale · Predation · Humpback whale · Rake marks · Fluke scarring · North Pacific

*Email: gsteiger@cascadiaresearch.org

INTRODUCTION

There has been considerable recent debate about the role of killer whale *Orcinus orca* predation on marine mammal populations in the North Pacific Ocean. Springer et al. (2003) suggest that the depletion of large whales during commercial whaling forced killer whales to prey more heavily on smaller marine mammals, thus triggering the sequential collapse of harbor seal *Phoca vitulina*, northern fur seal *Callorhinus ursinus*, Steller sea lion *Eumetopias jubatus*, and sea otter *Enhydra lutris* populations in the northern North Pacific and southern Bering Sea. This predation hypothesis assumes that large cetaceans were an important prey item of killer whales and that this predation occurred predominantly at their high-latitude feeding areas.

Killer whales have long been known to prey on marine mammals; Scammon (1874) recorded them feeding on gray whales *Eschrichtius robustus* in the mid-1800s. While attacks on large whales have been documented (Baldridge 1972, Whitehead & Glass 1985, Flórez-González et al. 1994, Goley & Straley 1994, George & Suydam 1998, Pitman et al. 2001, Ford et al. 2005), such observations are infrequent. Jefferson et al. (1991) summarized accounts of killer whales attacking or harassing 20 species of cetaceans, including humpback whales. Not all killer whales in the North Pacific attack marine mammals; 3 forms have been described, only one of which, colloquially termed 'transient,' preys upon marine mammals (Baird & Dill 1996, Ford et al. 1998).

Avoidance of predation by killer whales has been suggested to be the driving force behind the evolution of large whale migrations to low-latitude wintering grounds (Corkeron & Connor 1999). This migration hypothesis and the predation hypothesis (Springer et al. 2003) described above remain controversial and are the subject of continuing debate (Clapham 2001, Connor & Corkeron 2001, Williams et al. 2004, DeMaster et al. 2006, Mizroch & Rice 2006, Mehta et al. 2007, Reeves et al. 2007, Wade et al. 2007). An underlying question in these hypotheses is whether the killer whale predation was significant enough to have affected the behavior of large whale populations on an evolutionary time scale. Alternately, killer whales may have scavenged large whale carcasses as an artifact of commercial whaling operations (Whitehead & Reeves 2005).

Part of the problem in resolving these debates is the dearth of data on killer whale predation, with no direct evidence of the level of predation on large cetacean species. Because successful killer whale attacks are rarely witnessed, we examined evidence of non-lethal attacks by killer whales on large cetaceans discernable from parallel rake marks on the flukes from photo-identification studies. Rice & Wolman (1971) suggested that these rake mark scars are found predominantly on the flukes and flippers of whales because the killer whales seize these areas in an attempt to immobilize and drown their prey. Such marks have been reported for a number of large cetacean species (Rice & Wolman 1971, Katona et al. 1988, Kraus 1990, George et al. 1994, Naessig & Lanyon 2004). A recent study matching dentition patterns to scars has confirmed the long-held belief that such rake marks originate from killer whales (Mehta 2004). Off eastern Australia, about 17% of humpback whales had rake mark scarring from killer whales; most of these scars appeared to have been acquired when the humpbacks were young (Naessig & Lanyon 2004).

Photographs of the ventral sides of the flukes have been used to individually identify humpback whales for decades (e.g. Katona et al. 1979). Photo-identification studies of humpback whales in the North Pacific have revealed much about migrations, population structure and abundance (e.g. Darling & McSweeney 1985, Baker et al. 1986, Cerchio et al. 1998, Calambokidis et al. 2000, 2001, Urbán-R. et al. 2000, Calambokidis & Barlow 2004).

The population structure of humpback whales in the North Pacific is complex (Calambokidis et al. 2001). While humpback whales in this ocean demonstrate a high degree of site fidelity to specific feeding areas (from southern California to the Aleutian Islands and eastern Russia), feeding aggregations comprise animals from different wintering regions. Similarly, whales at wintering grounds (off Japan, Hawaii, mainland Mexico, Revillagigedo Archipelago and Central America) consist of whales from different feeding areas (Calambokidis et al. 2001).

We provide a large-scale overview of the incidence of scarring from killer whale attacks on humpback whales using an extensive sample of 16 wintering and feeding areas throughout the North Pacific basin. These data present a measure of regional differences in the rate of killer whale attacks on humpback whales and provide the best insights available on killer whale predation on humpback whales throughout the North Pacific. We use these analyses to address the effect of killer whale predation on humpback whales in the North Pacific and discuss implications for predation pressure in this ecosystem.

MATERIALS AND METHODS

A total of 6414 humpback whale fluke photographs taken between 1990 and 1993 were compiled from summer feeding and winter breeding areas in the North Pacific. Feeding areas sampled included the

coastal waters (offshore to approx. 50 nm) from southern California (32° N) to Prince William Sound (61° N) and as far west as the eastern Aleutian Islands (167° W); wintering regions included areas off Mexico (Baja, mainland Mexico and Revillagigedo Archipelago), Hawaii (Island of Hawaii, Maui and Kauai) and Japan (Okinawa and Ogasawara) (Fig. 1). The recently described wintering ground off Central America (Calambokidis et al. 2000) was not sampled at the time of this study. Our sample included all known feeding areas except those in the western Aleutian Islands and off Russia (not sampled at the time of this study). All photographs were graded and selected based upon quality criteria to evaluate the proportion of the fluke that was visible, fluke angle (i.e. how perpendicular it was to the water), the lateral angle of the photographer, the sharpness and grain, fluke size on the print, and the photographic quality (lighting, exposure and contrast) (Calambokidis et al. 2001). Photographs that did not meet our quality criteria were rejected. The entire sample of photographs was graded by one of 2 coders, both coded together using an archetype of each rake mark category.

In total, 3650 photographs of excellent quality were coded for the presence of killer whale rake marks (Table 1). This sample represented the best photograph of each individual whale from each area for each year. We allowed an individual animal to be represented in multiple regions (to avoid excluding it from a region) or in multiple years within a region because, in a few cases, the scar code was different either due to the rare instance of an individual that was attacked during the study period or differences in the quality of the photographs. We chose to include these duplicates to avoid bias introduced by making a selection among them. We also verified that exclusion of these duplicate sightings of the same individual neither altered the percentage of animals with rake marks by region nor affected results of any of the statistical analyses.

A rake mark scar was defined as a set of 3 or more parallel lines or marks in close proximity. Lighting and exposure in photographs were critical to the visibility of faint scars. We coded fluke photographs for the presence of rake marks using 5 categories (Fig. 2): (1) rake marks with injuries that inflicted damage to the integrity of the fluke, (2) severe scarring (3 or more sets of rake marks), (3) 1 to 2 sets of rake marks present, (4) scratches that were possibly caused by killer whale teeth but did not meet the definition of 3 parallel lines in close proximity, and (5) no rake marks were visible.

Fig. 1. Study area showing the locations where photographs were taken. PWS: Prince William Sound; SE AK: southeastern Alaska; n. Brit Col: northern British Columbia); s. Brit Col: southern British Columbia

Table 1. *Megaptera novaeangliae*. Summary of the sample used. Photographs were taken between 1990 and 1993

| Region	Photos selected	Unique IDs	Collector
Mexico			
Mainland Mexico	139	138	Univ. Nacional Autonoma de Mexico (UNAM)
Baja California	255	233	Univ. Autonoma de Baja California Sur (UABCS)
Revillagigedo Archipelago	168	159	J. Jacobsen, UNAM, UABCS
Hawaii			
Island of Hawaii	433	401	Kewalo Basin Marine Lab (Univ. of Hawaii)
Maui	393	368	Hawaii Whale Research Foundation
Kauai	386	375	S. Cerchio
Japan			
Ogasawara	360	257	Ogasawara Marine Center
Okinawa	88	63	Okinawa Expo Aquarium, WWF-Japan
US West Coast			
California–Washington	694	454	Cascadia Research Collective (CRC)
British Columbia, Canada			
Southern Vancouver Island	13	14	Center for Whale Research, CRC
Northern British Columbia	64	59	Fisheries and Oceans, Canada
Alaska			
Southeastern Alaska	421	287	Glacier Bay National Park, J. Straley
Prince William Sound	135	87	North Gulf Oceanic Society (NGOS)
Kodiak Island	79	76	National Marine Mammal Lab (NMML), NGOS
Shumagin Islands	15	15	NMML
Bering Sea	7	7	NMML
Total	3650	2993	
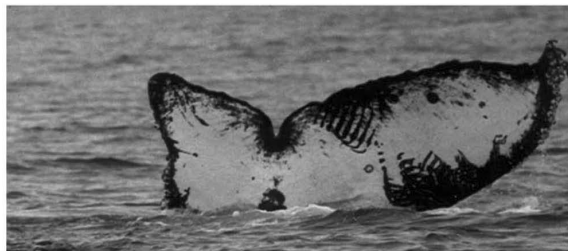
Category 1

Category 4

Category 2
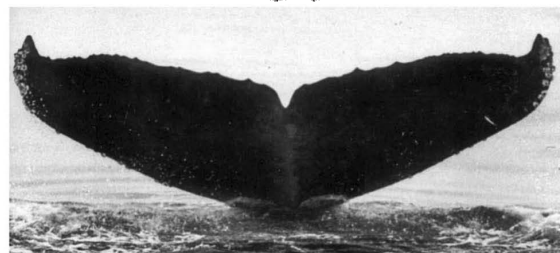
Category 5

Category 3

Fig. 2. *Megaptera novaeangliae*. Examples of rake mark scarring categories. Photographs were taken by J.C., K.C.B., Todd Chandler and Joe Evenson

For damaged flukes in Category 1, rake marks had to be visibly associated with the injury for it to be scored. Flukes with damage and no rake marks were counted in the no rake mark category (Category 5). For our analyses, we combined Categories 1 to 3 to examine the total number of animals with rake mark scars (excluding those with possible rake mark scars).

The majority of rake mark scars seen on humpback whale flukes in this study were very likely caused by the grasping and scraping of the conical teeth of killer whales, although we did not measure the distance between each rake scar on our photographs. The scars we describe here are consistent in appearance with those documented by George et al. (1994) on hunted bowhead whales *Balaena mysticetus*. These authors reported that killer whale rake marks were parallel scars 2.5 to 5.1 cm apart, measuring 1 cm in width. The scars that we observed were dissimilar to the arc-shaped jagged scars that are attributed to sharks (Brodie & Beck 1983, George et al. 1994, Naessig & Lanyon 2004). It is possible that some of the rake mark scars were caused by smaller odontocetes, such as false killer whales *Pseudorca crassidens*, which are known to occasionally bite large cetaceans (Palacios & Mate 1996, Weller 2002, Naessig & Lanyon 2004), but from our subjective observations of scar size, these were rare.

The incidence of scarring we report here is conservative and probably underestimates the true proportion of non-lethal attacks. Despite our strict quality criteria,

we found a few cases where faint rake marks were not seen in a photograph of an individual but were visible in others when lighting and exposure were optimal.

RESULTS

Overall, 15 % (562 of 3650) of fluke photographs examined for all North Pacific regions had unambiguous, discernable rake mark scars (Table 2). Of those with these scars, 20 % had damaged flukes with missing pieces associated with the rake marks. Most (60 %) of the whales with rake marks had 1 or 2 sets of rake marks present.

When data were pooled, humpback whales on the 3 primary wintering grounds (Mexico, Hawaii, and Japan) had a significantly higher proportion of rake marks on their flukes than those sampled on the feeding grounds ($\chi^2 = 10.7$, df = 1, p = 0.001). Significant differences were also found in the proportion of whales with rake mark scarring among North Pacific feeding grounds ($\chi^2 = 58.5$, df = 4, p < 0.001) and among wintering regions ($\chi^2 = 62.1$, df = 2, p < 0.001).

The incidence of rake marks for whales off California–Washington (20 %) was at least twice as high as any other feeding region (5 to 9 %, Fig. 3). While the lowest incidence of rake marks in feeding areas occurred off British Columbia (5 %) and off southeastern Alaska (6 %), there were no significant differences

Table 2. *Megaptera novaeangliae.* Rake mark scarring results (n = 3650) by region. Scarring categories were: (1) damaged flukes, (2) 3 or more sets of rake marks, (3) 1 to 2 sets of rake marks, (4) possible rake marks, (5) no rake marks

Region	No. of photos	Scarring category With rake marks					Total with rake marks Categories 1–3		
		1	2	3	4[a]	5	No.	%	SE (%)
Mainland Mexico	139	14	10	19	30	66	43	31	4
Baja	255	15	20	24	38	158	59	23	3
Revillagigedos	168	12	10	22	44	80	44	26	3
Island of Hawaii	433	9	23	48	102	251	80	18	2
Maui	393	9	10	40	56	278	59	15	2
Kauai	386	14	9	36	74	253	59	15	2
Ogasawara	360	4	2	22	80	252	28	8	1
Okinawa	88	0	2	3	19	64	5	6	2
All wintering regions (pooled)	2222	77	86	214	443	1402	377	17	1
Avg. of all wintering regions								18	
California–Washington	694	32	18	88	126	430	138	20	2
British Columbia	77	0	1	3	8	65	4	5	3
SE Alaska	421	0	3	21	106	291	24	6	1
Prince William Sound	135	3	3	6	19	104	12	9	2
Kodiak-Aleut-Bering	101	0	1	6	9	85	7	7	3
All feeding areas (pooled)	1428	35	26	124	268	975	185	13	1
Avg. of all feeding areas								9	
All areas (pooled)	3650	112	112	338	711	2377	562	15	1
Avg. of all areas								15	

[a]Scars that were possibly caused by killer whale teeth but did not meet the definition of 3 parallel lines in close proximity
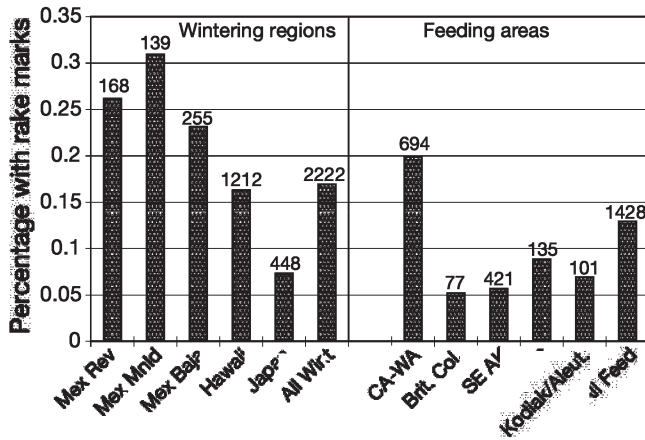
Fig. 3. *Megaptera novaeangliae*. Incidence of rake mark scarring on humpback whale flukes by region. Number of photographs is given above bars. Areas were pooled for Hawaii (Maui, Kauai and Hawaii) and Japan (Ogasawara and Okinawa). Mex Rev: Mexico Revillagigedos; Mex Mnld: Mexico Mainland; Mex Baja: Mexico Baja; All Wint: all wintering areas; CA-WA: California– Washington; Brit. Col.: British Columbia; SE AK: southeastern Alaska; PWS: Prince William Sound; All Feed: all feeding areas

among feeding areas when California-Washington was excluded (χ^2 = 2.0, df = 3, p = 0.578). For wintering regions, rake mark scars were more prevalent on whales off Mexico (26%) than those at other wintering areas (Japan 7%, Hawaii 16%, Fig. 3). While lower than Mexico, Japan and Hawaii were still significantly different from each other (χ^2 =21.9, df = 1, p < 0.001). The proportion of rake marks on whales in all areas off Mexico was high (Baja 23%, mainland Mexico 31%, Revillagigedos 26%). There were no significant differences among areas within any of the 3 wintering grounds (χ^2 test, p > 0.05 in all 3 cases).

DISCUSSION

It is useful to examine rake mark scarring as an indicator of killer whale attacks because so few attacks are actually witnessed. Jefferson et al. (1991) reported only 12 accounts of killer whale attacks on humpback whales since the mid-1800s worldwide. Similarly, in an 'extensive (but not exhaustive) review' of literature going back as far as 1840 through 1968, Mizroch & Rice (2006) found 11 accounts of killer whale attacks on whales in the North Pacific; none of these attacks were on humpback whales. However, the high prevalence of rake mark scarring in recent decades demonstrates that in some areas (e.g. whales off Mexico), as many as a third of all animals have survived an attack at least once. Considering the long lifespan of a humpback whale (approx. 90 yr, estimated from Chittlebor-

ough 1959), the proportion of time that a whale is under threat of attack over its lifetime may be small. Because it appears that most attacks appear to occur when whales are calves (Clapham 1996, Naessig & Lanyon 2004, Mehta et al. 2007), the high prevalence of rake mark scarring in some areas indicates that predation could be a significant source of calf mortality, particularly in some regions.

Killer whales would not risk the physical danger and energy expenditure of attacks on humpback whales without the benefit of a fair amount of success. The flukes of large whales are powerful and, for the killer whale, there is substantial risk associated with attacks on this species. A bowhead whale was observed to kill a killer whale by hitting it with its fluke (Eschricht 1866), and a gray whale was reported to use its fluke to kill a walrus *Odobenus rosmarus* (Mazzone 1987). For this reason, we believe that when killer whales actually bite the flukes of a large cetacean (causing rake mark scars), these encounters are largely predatory attacks.

Rake mark scarring is a complex combination of a number of factors: the attack rate, escape rate and long-term behavior of the animals that survive attacks. While scarring data are not an unequivocal measure of successful predation, we know that the population with the highest incidence of rake marks is the population that survives the greatest number of killer whale attacks. We assume that the rate of unsuccessful attacks (as indicated by rake marks) reflects the degree of predatory pressure and is correlated with the rate of overall attacks. While a study of the survivors of attacks presents potential biases, we believe that our data present a reasonable measure of regional differences in the rate of attacks on humpback whales throughout the North Pacific Ocean.

The rate of attacks and the incidence of unsuccessful attempts (revealed by rake marks on the flukes) would vary by the prey species. The large cetacean species that tend to resist attacks by thrashing their flukes (e.g. humpback or sperm whales, Weller 2002), would probably be more likely to survive attacks (with rake marks on their flukes) than those with more submissive physical reactions, that are less able to fight back in response to attacks (e.g. minke whales, Ford et al. 2005). The 2 large cetacean species considered to be most frequently killed by killer whales, i.e. gray and bowhead whales (Reeves et al. 2007), however, are species on which rake marks on survivors are also commonly seen (George et al. 1994, Weller 2002).

Several demographic, temporal and behavioral factors may influence our findings of overall higher prevalence of rake marks found on whales at the wintering grounds compared to feeding areas. Wintering ground samples are less representative of the entire popula-

tion than feeding area samples (Clapham et al. 1995), where males are more likely to return and are present in greater numbers than females (Brown et al. 1995, Craig & Herman 1997, Smith et al. 1999) and juveniles are probably underrepresented (Robbins 2007). Wintering-ground samples could also be biased because of habitat preferences and differences in migratory timing related to age, sex and reproductive status (Smultea 1994, Brown et al. 1995, Craig & Herman 2000, Craig et al. 2003). Changes in the rate of killer whale attacks over time would affect the proportion of animals with rake marks when the sample is skewed by age class. If killer whale attacks were to occur primarily at or near breeding grounds (as we suggest below), then males and older animals that spend longer periods on the breeding grounds might be more subject to attack there. Because we believe that calves are the primary targets of predation (Naessig & Lanyon 2004, Mehta et al. 2007), the impact of longer tenure on breeding grounds would only have a small effect. It is also possible that attacked animals may behave or be distributed differently. At this point, we cannot resolve to what degree these factors affect the higher observed incidence of rake marks on the breeding areas compared to the feeding grounds.

The overall proportion of humpback whales with rake mark scars for the entire North Pacific sample was within the range of 14 to 20% of whales with rake mark scars reported in the North Atlantic (Katona et al. 1988) and off eastern Australia (Naessig & Lanyon 2004). However, the incidence of animals we observed with rake marks in specific areas (7 to 31% in wintering grounds and 5 to 20% in feeding areas) often fell outside the ranges reported previously. Clearly, humpback whales in different regions within the North Pacific are exposed to very different levels of predation and general assumptions regarding predation pressure should take into account such regional differences. For example, Dolphin (1987) draws conclusions about predator–prey relationships based on the lack of killer whale attacks on humpback whales in southeastern Alaska, an area where the incidence of rake mark scars was low (6%).

That whales off California and Mexico had the highest rate of rake marks is consistent with the migratory connection between these areas; mainland Mexico and Baja are primary migratory destinations for humpback whales off California (Urbán-R. et al. 2000, Calambokidis et al. 2000, 2001). While mammal-eating killer whales occur in both regions (Black et al. 1997), our evidence suggests that most attacks occur on or near the Mexican wintering grounds (Fig. 3). All 3 Mexican wintering areas showed a similarly high incidence of rake marks, even though whales in these areas have different migratory destinations. The incidence of rake

marks on humpback whales that winter in the offshore Mexican waters of the Revillagigedo Archipelago (26%) and those off mainland Mexico (31%) are both high, even though few humpback whales from the Revillagigedos migrate to California (Urbán-R. et al. 2000, Calambokidis et al. 2000, 2001). If the high incidence of rake marks on humpback whales off Mexico were the result of attacks off California, then we would expect the proportion of scarred whales off mainland Mexico to be substantially higher than those at the Revillagigedo Archipelago.

The high prevalence of killer whale rake mark scars on humpback whales off California and Mexico is in contrast to the relatively low density of killer whales in these 2 regions compared to higher latitudes. Overall, killer whales are more abundant at higher latitudes than in tropical waters; in the North Pacific, killer whale densities off Central America, Mexico, and California (0.02 to 0.06 ind. 100 km^{-2}) are substantially lower than feeding areas to the north, including Oregon and Washington, British Columbia, and Alaskan waters (0.19 to 0.68 ind. 100 km^{-2}, except for the central Bering Sea estimate of 0.06) (Forney & Wade 2007). We suggest that killer whales in tropical waters are more selectively targeting humpback whales seasonally and, while the density of killer whales overall may be lower, the percentage of animals that prey on whales may be high.

Selective prey choice on baleen whales by killer whales off California and Mexico may reflect the presence of large numbers of both humpback and gray whale calves in this region. The waters off Mexico are unique in that they are calving grounds for both gray and humpback whales (Rice & Wolman 1971, Urbán-R. & Aguayo 1987, Urbán-R. et al. 2003). Both species follow a similar migratory path in coastal waters off Baja California and California; gray whale calves are born off southern Baja California in winter (Rice et al. 1981, Urbán-R. et al. 2003) and migrate northward along the California coast in spring (Poole 1984), this coastal migration route is also used by humpback whales and their calves traveling to feeding grounds of the US West Coast (Urbán-R. et al. 2000). For tropical waters, Baird (2002) hypothesized that killer whales in areas of low productivity have a broader diet than those in high latitudes, where prey specialization is generally seen. Killer whale predation on newborn calves would involve a lower energetic cost and less risk than predation on older animals. This is supported by the rake mark data, which show that most scarring occurs in the first year of life (Naessig & Lanyon 2004).

The premise of the Corkeron & Connor (1999) migration hypothesis is that, for pregnant baleen whales, the major selective advantage of migration is to reduce the risk of killer whale predation on newborn calves. Our

data suggest that a substantial proportion of humpback whales are affected by predation attempts; this would support Corkeron & Conner's hypothesis. However, our inference that the majority of attacks occur on the wintering grounds is contrary to the predictions of Corkeron & Connor (1999). Our data show that humpback whales are not currently avoiding this risk by migrating to tropical waters in the eastern North Pacific, although it is impossible to predict the rate of attack that humpback whale calves would experience if born during winter on the feeding grounds. In response to criticism by Clapham (2001) that killer whale attacks were not common in feeding areas, Connor & Corkeron (2001) stated that their hypothesis addressed the distal causes of migration in evolutionary history, when killer whale attacks might have been more prevalent in the high-latitude feeding areas. Current migratory behavior, then, might be derived from the early selection of those animals that avoided predation by migrating, even if this strategy may not appear to be effective at this time. The prevalence of rake mark scars in some regions supports the possibility that predation on calves could be a factor that has affected the behavior of large whales.

Evidence from the US West Coast is inconsistent with the hypothesis that the depletion of large whale populations during commercial whaling forced killer whales to shift their predation to smaller prey, thus triggering the sequential collapse of pinniped and sea otter populations (as Springer et al. 2003 hypothesized for western Alaska). Along the US and Mexico west coasts, while humpback and gray whales were severely depleted through the mid-1960s (Rice 1963, Clapham et al. 1997), this region has experienced substantial increases in pinniped populations (summarized by Wade et al. 2006). Additionally, our inference that most attacks occur on or near the wintering grounds (and that whales from the Alaskan coast have relatively low levels of scarring) is inconsistent with a primary assertion of Springer et al.'s (2003) hypothesis that killer whales, at least historically, preyed heavily on large whales in high-latitude feeding areas such as the Bering Sea. While this might not be the case if killer whales selected to feed on the carcasses from whales killed or injured during whaling (as suggested by Whitehead & Reeves 2005), it is still not clear why this also would not have occurred off the US West Coast and caused a collapse of pinniped populations there.

Because humpback whale numbers in the North Pacific appear to be increasing (Calambokidis et al. 1997), it seems that killer whale predation is not having a significant impact on these populations. Overall basin-wide estimates of the abundance of humpback whales in the North Pacific were estimated as 6010

(SE = 474) in the early 1990s and appeared to be increasing as they recovered from commercial whaling (Calambokidis et al. 1997). Abundance estimates show an increasing trend of about 8% per year for the California–Oregon–Washington feeding aggregation (Calambokidis & Barlow 2004) and 10% per annum for the population that migrates between Hawaii and Alaska (Mizroch et al. 2004, Cerchio 1998). We cannot dismiss completely, however, the potential for some effect of predation on the rate of increase; the observed proportion of humpback whale calves in the US West Coast feeding area is lower than other humpback whale populations, although this could be biased by the timing of observations (Steiger & Calambokidis 2000).

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