

Scientific Information and technical references on particular aspects of Killer Whales (Orcinus orca).

*Wissenschaftliche Informationen und Fachspezifische
Bezüge zu Einzelnen Aspekten von Schwertwalen
(Orcinus Orca)*

August 2015



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Rake Marks / Bissspuren

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1.3 Scientific description of rake marks in wild dolphins

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Beispiele von Bissspuren bei wilden Schwertwalen aus Identifikationskatalogen.

1.1

Introduction / Einleitung

Rake marks are normal features in wild killer whales, and in all the toothed whales (*Odontocete*) species. These scratches are produced by the normal social interaction between individuals of the group, during agonistic interactions (aggressions) one animal can leave marks on the skin of another with his teeth.

These marks are well known by cetacean scientists, and also by the crews of the whale-watching boats. In killer whales this marks have been scientifically documented in several occasions, for example by Ingrid Visser (Free Morgan Foundation) who found two individuals prolifically raked in New Zealand almost 20 years ago (See 1.2)

Despite the arguments of wild cetaceans able to swim out to avoid conflicts in the wild (never described in the scientific literature), the intensity of rakes in wild dolphins have been used to monitor aggressive behaviour. (See 1.3)

Rake marks in wild killer whales are so very common that they can be easily found in killer whale ID catalogues (See 1.4)

Rake marks can only be considered a health problem when there is poor water quality (for example in heavily polluted coastal areas). Loro Parque has a water quality system that has been accredited by the Animal and Plant Health Inspection Service of the United States to exceed the standards in place in the cetacean facilities in the USA. Water quality is controlled daily, and bacteriological tests are run twice a week to ensure that it is free of pathogenic microorganisms. As a result the potential deleterious effect of the rake marks on the health of these killer whales is negligible.

Bissspuren sind sowohl bei wilden Schwertwalen als auch bei allen anderen Zahnwalen (*Odontoceti*) völlig normale Merkmale. Diese Schrammen und Kratzer entstehen im Laufe der normalen sozialen Interaktion der Gruppenmitglieder. Wenn es zu agonistischen Interaktionen, also Aggressionen kommt, ist es durchaus üblich, dass die Tiere mit ihren Zähnen Spuren auf der Haut eines anderen Tieres hinterlassen.

Diese Kratzer und Narben sind unter Walforschern und bei den Besatzungen von Walbeobachtungsbooten sehr bekannt. Bei Schwertwalen wurden diese Bissspuren bereits mehrmals wissenschaftlich dokumentiert – zum Beispiel von Ingrid Visser (Free Morgan Foundation), die vor fast 20 Jahren in Neuseeland zwei Exemplare sichtete, welche besonders viele Narben aufwiesen. (siehe 1.2)

Trotz der Argumente, dass wilde Walarten in freier Wildbahn in der Lage sind, sich gegenseitig aus dem Weg zu gehen, um Konflikte zu vermeiden (was nie in der wissenschaftlichen Literatur beschrieben wurde), wurde das Ausmaß der Bissspuren bei wilden Delfinen dennoch zur Beobachtung und Beurteilung von aggressivem Verhalten verwendet. (siehe 1.3)

Bissspuren bei wilden Schwertwalen sind so häufig, dass sie leicht in Schwertwal-Identifikationskatalogen zu finden sind. (siehe 1.4)

Bissspuren können nur bei mangelnder Wasserqualität (zum Beispiel in stark verschmutzten Küstengebieten) als Gesundheitsproblem angesehen werden. Der Loro Parque verfügt über ein Wasserqualitätssystem, das laut dem amtlichen Tier- und Pflanzenschutzdienst der Vereinigten Staaten von Amerika die höchsten Standards von Einrichtungen in den USA sogar noch übertrifft. Die Wasserqualität wird täglich kontrolliert und zweimal pro Woche werden bakteriologische Tests durchgeführt, die sicherstellen, dass das Wasser frei von krankheitserregenden Mikroorganismen ist. Demzufolge sind die potenziellen schädlichen Auswirkungen der Bissspuren auf die Gesundheit dieser Schwertwale unerheblich.

Aquatic Mammals 1998, **24.2**, 71-81

Prolific body scars and collapsing dorsal fins on killer whales (*Orcinus orca*) in New Zealand waters

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Summary

An account is given of adult male killer whales (*Orcinus orca*) in New Zealand waters, where two whales have prolific scars caused by conspecifics and seven whales have collapsing, collapsed or bent dorsal fins (23% of the observed New Zealand adult male killer whale population).

Introduction

Scars on the bodies of cetaceans have been reported for a wide range of species. In general, these scars are attributed to teeth marks from conspecifics, e.g., bottlenose dolphin *Tursiops truncatus* (Gunter, 1942), pygmy sperm whale *Kogia breviceps* (McCann, 1974), sperm whale *Physeter macrocephalus* (Kato, 1984), Risso's dolphin *Grampus griseus* (McCann, 1974), striped dolphin *Stenella coeruleoalba* (Mitchell, 1970), long finned pilot whale *Globicephala melas* (McCann, 1974) and narwhal *Monodon monoceros* (Sliveman & Dunbar, 1980), which have also been reported with tusks from conspecifics embedded in muscle tissue (Ford & Ford, 1986; Geist *et al.*, 1960). Scars have also been reported on various beaked whales; Baird's *Berardius bairdii* (Omura *et al.*, 1955), Hubb's *Mesoplodon carlhubbsi* (Heyning, 1984), Cuvier's *Ziphius cavirostris* (Heyning, 1989), True's *Mesoplodon mirus* T. Pusser, (pers. comm.), Bowdoin's *Mesoplodon bowdoini* (Hubbs, 1946), dense beaked *Mesoplodon densirostris* (Heyning, 1984), Arnoux's *Berardius arnouxii* (McCann, 1974), and Gray's *Mesoplodon grayi* (pers. obs). Limited literature refers to scars on killer whales (Ford *et al.*, 1994; Hoyt, 1984; Scheffer, 1969).

Collapsing, collapsed or bent dorsal fins of killer whales have only been reported in passing in the literature, although a few photographs have been published (Baird & Stacey, 1989; Ford *et al.*, 1994; Hoyt, 1984; Matkin, 1994). The purpose of this paper is to describe prolific body scars and collapsing, collapsed or bent dorsal fins on a number of

killer whales found in New Zealand waters. Few accounts of killer whales with body scars or abnormal dorsal fins have been reported worldwide, and these are the first from New Zealand.

Methods

The observations reported here were collected as part of a long term study of the killer whale population found in the waters around New Zealand. To date (September 1997) 125 individuals have been photoidentified, using methods developed by Bigg (1987). Data were collected in an opportunistic manner, including photographs of killer whales from the public. Killer whales were encountered after a report from fishermen, whale and dolphin watching boats, coastguard or the public and were followed until such constraints as fuel, weather conditions, or the animals' behaviour caused the encounter to be terminated. Where possible, photographs of killer whales were taken using a Nikon F90 camera with a 80-200 lens and Kodak 100 Select transparency film. A 4.3 m rigid hull inflatable with a 60 hp outboard engine was used as the observation platform and locations were recorded from nautical charts and/or a hand-held Global Positioning System (GPS).

Identified killer whales were assigned a category based on sex and/or age. All animals reported here fall into the category 'Adult Male'—categorised by having distinctively large dorsal fins (Bigg, 1982). For the purpose of this paper, 'prolific body scars' refers to scars on the killer whales that are extensive and numerous. These scars are generally parallel rows of three or four per group. The collapsing, collapsed or bent dorsal fins refer to a fin that is, or has begun to hang to one side of the animal's body, or is no longer upright. It may also have some form of malformation such as a bend or wave, or a combination of both hanging and bending. These dorsal fins are referred to as 'abnormal'.

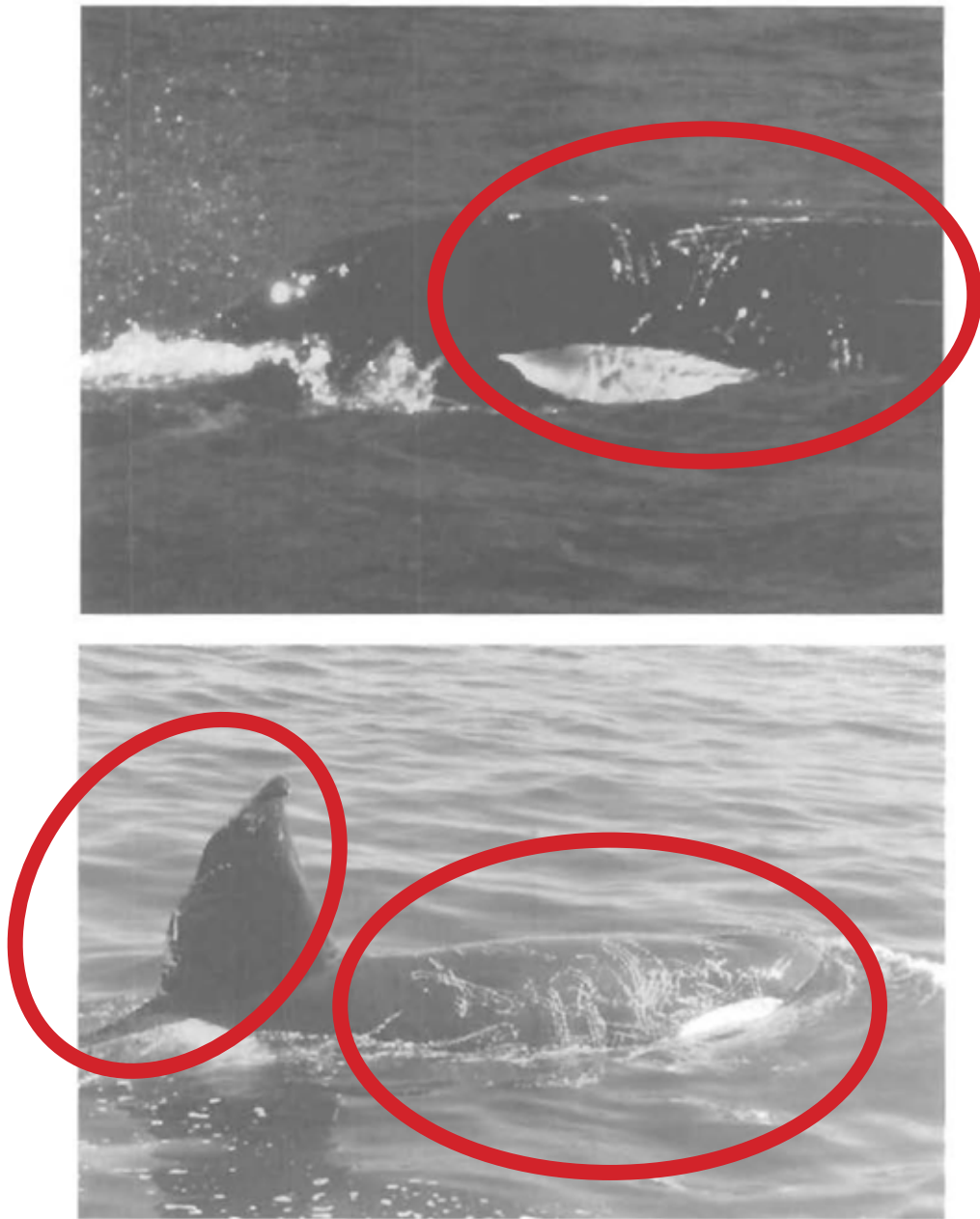


Figure 1 (a) Scarring on the eye patch area of NZ26, where loose pieces of skin can be seen (photo author), (b) Prolific scarring on the dorso-lateral area of NZ26, which is raised into 'welts' (photo P. & K. Waller).

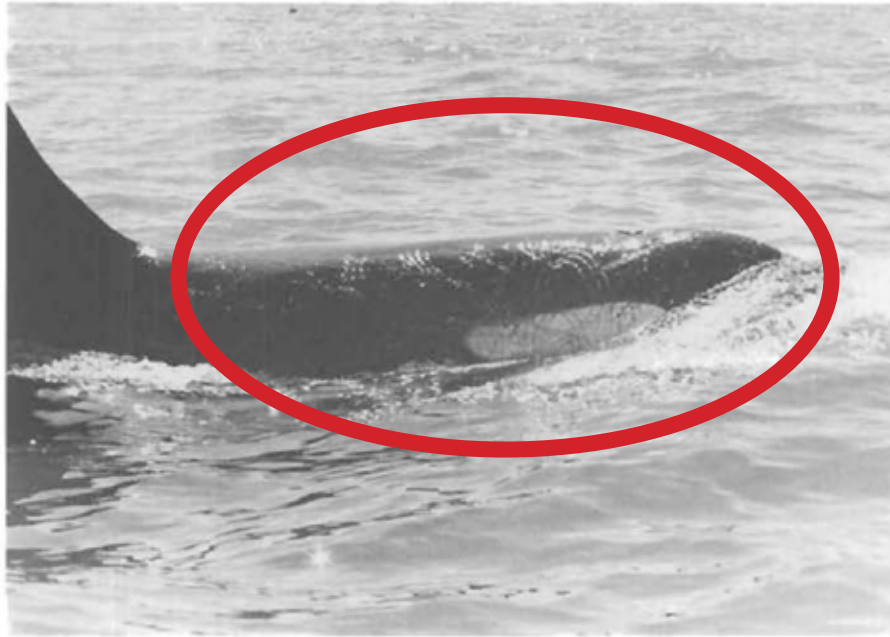


Figure 2. Prolific scarring on the dorso-lateral area of NZ85, showing contrasting colour on eye patch area (photo D. Buurman).

Using Tooth Rakes to Monitor Population and Sex Differences in Aggressive Behaviour in Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

This study investigated intraspecific tooth rake scarring, an established indicator of received aggression by conspecifics, on bottlenose dolphins (*Tursiops truncatus*) to gain knowledge of aggressive interactions. The differences in tooth rake scarring between male and female dolphins on the east coast of Scotland were examined, and overall levels of scarring were compared with dolphins on the west coast of Scotland (Sound of Barra and Hebrides). Photographs were examined for evidence of tooth rake scarring using four different methods. East coast males displayed significantly higher scarring percentages (i.e., body area covered by tooth rake scarring), numbers of dorsal fin rake directions (i.e., whether tooth rake scars were vertical, horizontal, diagonal, or curved), and nick percentage (i.e., amount of the dorsal fin missing due to nicks) than females. Differences also existed between the three areas, with bottlenose dolphins around the Sound of Barra showing significantly lower levels of dorsal fin rake directions than those on the east coast or Hebrides. Observed sex differences are likely the result of intrasexual conflict between males over access to females. However, other factors such as sex- or age-specific behaviours or sexual coercion of females may also be involved. Such information could potentially be used to differentiate between the sexes. The differences in dorsal fin scarring between these populations suggests differences in aggressive interactions, possibly indicating differences in social structure. The lower scarring levels seen in the Sound of Barra group may support the suggestion that bottlenose dolphins on the west coast belong to two communities. However, this variability in conspecific aggression may also be the result of different social behaviours, age or sex ratios, habitat, resources, or individual behavioural differences.

Key Words: social behaviour, social structure, cetacean, intraspecific aggression, tooth rake scarring, bottlenose dolphin, *Tursiops truncatus*

Introduction

Aggression is found throughout the animal kingdom, in both solitary and group-living species, and can occur for a number of reasons, most commonly as a response to intrasexual competition or intersexual conflict. For cetaceans, however, which spend the majority of their lives submerged, aggressive events are difficult to observe.

Much of our knowledge regarding dolphin aggression has been gained through studies of captive bottlenose dolphins (*Tursiops* sp.) (Tyack, 2000). Bottlenose dolphins are known to employ a range of aggressive behaviour in their social interactions, including chasing, ramming, body slamming, sideswipes, tail slaps, and biting (Samuels & Gifford, 1997; Weaver, 2003). Furthermore, other behaviours have been categorised as submissive (e.g., swimming ventral to an aggressor and affiliative rubbing), providing information about the winners and losers of such interactions (Samuels & Gifford, 1997). However, animals in one captive facility may not necessarily display the same behaviour as animals in a different facility. Additionally, and perhaps more importantly, data from captive studies may not show parallels with wild populations (Tyack, 2000).

Studies of aggression in wild bottlenose dolphins have generally used information from stranded animals (Patterson et al., 1998), from one or more direct observations (Parsons et al., 2003a; Cotter et al., 2011), or from interspecific interactions (Ross & Wilson, 1996; Herzing et al., 2003). Scars and natural markings have been used for individual identification of cetaceans (Würsig & Jefferson, 1990). These natural marks (e.g., tooth rake scars and nicks) are often inflicted during agonistic interactions with conspecifics. They can therefore be used as an indirect indicator of intraspecific aggression in the wild.

Tolley et al. (1995) investigated sexual dimorphism in wild bottlenose dolphins (*Tursiops truncatus*) using photographs to compare the frequency

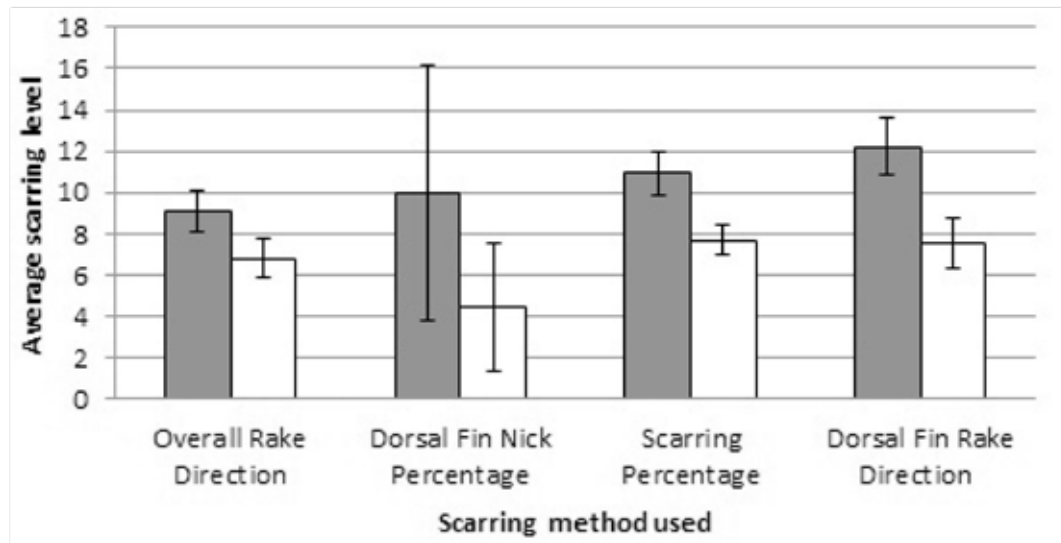


Figure 3. Average degree of scarring for known-sex individuals ($n = 27$) from the east coast of Scotland bottlenose dolphin population: males ($n = 9$; dark grey) and females ($n = 18$; white)

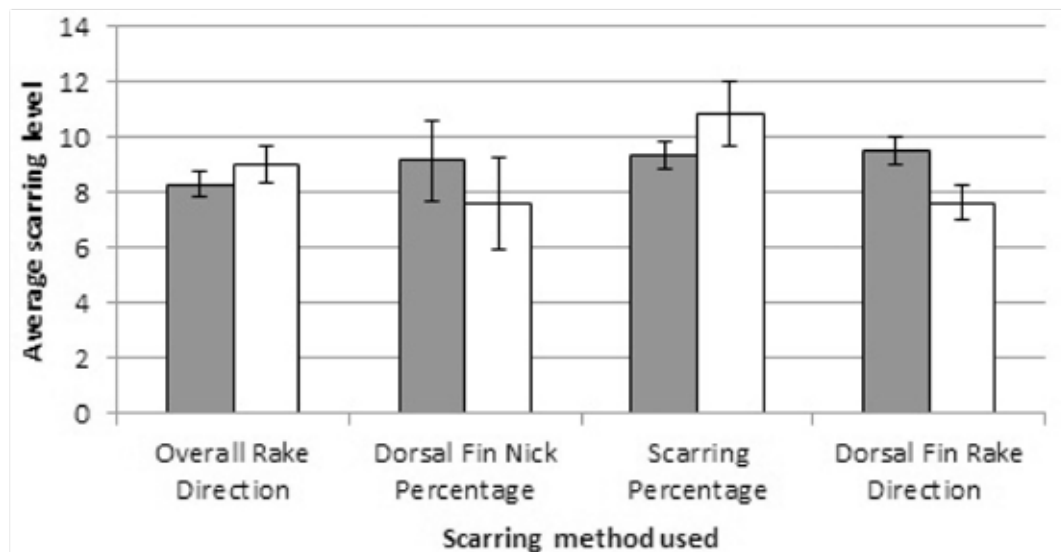


Figure 4. A comparison of average degree of scarring between the east coast ($n = 76$; dark grey) and west coast ($n = 35$; white) populations

behaviour between the sexes and indicates that scarring could potentially be used to determine the sex of individuals. Differences also exist between the three groups, with bottlenose dolphins seen around the Sound of Barra, the smallest group, exhibiting the lowest levels of scarring. This suggests there are also differences in intraspecific aggression between these different populations and areas.

Differences in Scarring Quantification Techniques

As demonstrated in this study, the application of different methods for quantifying tooth rake scarring can produce different results. The dorsal fin appears to be a likely body part to show scarring during aggressive interactions, possibly as bottlenose dolphins may turn their dorsal side (a less vulnerable area) to attacks. Similarly, SP perhaps signifies the intensity of such interactions; a few rakes

of social bonds. Bottlenose dolphins seen around the Sound of Barra have not been known to interact with the other bottlenose dolphins on the west coast, and this group contains the smallest number of bottlenose dolphins (Grellier & Wilson, 2003; Cheney et al., 2013). This small group may have more stable social bonds or, as they do not mix with other groups, may have less inter-group conflict. However, differences in scarring could also be a result of different age or sex ratios, habitat, resources, or individual behavioural differences between these groups that could affect aggressive interactions and/or the degree of scarring.

Conclusion

As aggressive events are difficult to observe in dolphins in the wild, the use of tooth rake scars as indicators of intraspecific aggression among bottlenose dolphins may be a good source of information. The type of scarring exhibited by an individual may indicate the degree of aggression to which a particular individual might be involved. Thus, examining differences in scarring prevalence and type may highlight differences in social behaviour and in other aspects of ecology among different sexes or populations. East coast males appear to be more heavily scarred than females. This sex bias suggests that individuals could potentially be provisionally sexed according to their scarring levels. These scarring differences also suggest differences in social behaviour; however, the exact cause is yet to be determined. Two techniques (ORD and DFRD), which both examine rake direction, repeatedly highlighted dividing factors between the populations. Despite the fact that the three groups of dolphins around Scotland are the same species, there are significant variations in scarring levels, implying social differences between these populations.

Acknowledgments

The core bottlenose dolphin photo-identification study was conducted in collaboration with the Sea Mammal Research Unit at the University of St Andrews. We thank Susan Lusseau, Simon Ingram, Ross Culloch, and many other colleagues who contributed to the challenging fieldwork required to collect these data. The success of photo-identification on the west coast of Scotland depended upon collaboration with the Scottish Association for Marine Science, the Hebridean Whale and Dolphin Trust, and all the members of the public that reported bottlenose dolphin sightings. Many aspects of this study have also benefited from close integration with related projects that have been funded from a variety of sources. In particular, we thank the Scottish Government,

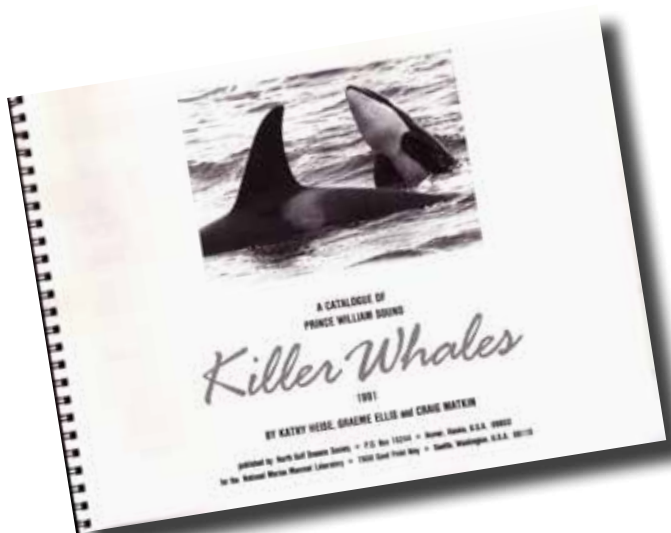
Scottish Natural Heritage (SNH), the Whale and Dolphin Conservation Society, Talisman Energy (UK) Ltd, Chevron, the European Union, and the Natural Environment Research Council. Thanks also to SNH for granting Animal Scientific Licences to carry out this work.

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1.4

Examples of rake marks in wild killer whales Beispiele von Bissspuren bei Schwertwalen



Rake marks in wild killer whales are so very common that they can be easily found in classic killer whale ID catalogues, in the new ID catalogues online (<http://northernresidentorcas.tumblr.com>) or even on the websites of whale-watching companies or orca conservation NGOs.



Bissspuren bei wilden Schwertwalen sind so häufig, dass sie problemlos in klassischen Schwertwal-Identifikationskatalogen, in den neuen Identifikationskatalogen online (<http://northernresidentorcas.tumblr.com>) oder sogar auf den Internetseiten von Walbeobachtungsunternehmen oder Nichtregierungsorganisationen, die sich für den Naturschutz einsetzen, zu finden sind.





Individual / Exemplar:

AB 6 (Foreground / Delante)

AB 37 (Background / Atrás)

Date / Datum :

11 May 1986 / 11 de mayo de 1986

Author / Urheber:

Craig Matkin

Note / Anmerkung:

Heavily raked calf not identified in the original publication, possibly AB 37 / Cría con un enorme número de marcas, el ejemplar podría ser AB37 aunque no se identifica en la publicación original.

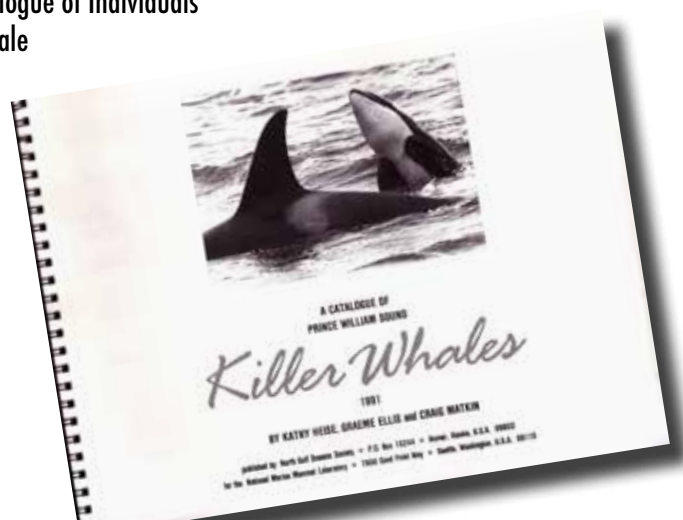
Photo-Identification Catalog / Foto-Identifikationskatalog:

Killer whales of Prince William Sound and Southeast Alaska A Catalogue of Individuals

Photoidentified, 1976-1986. Edited By Graeme Ellis. West Coast Whale

Research Foundation. 1040 West Georgia Street, Room 2020.

Vancouver, British Columbia.





Individual / Exemplar:

AB 37 (Foreground / Delante)

AB 6 (Background / Atrás)

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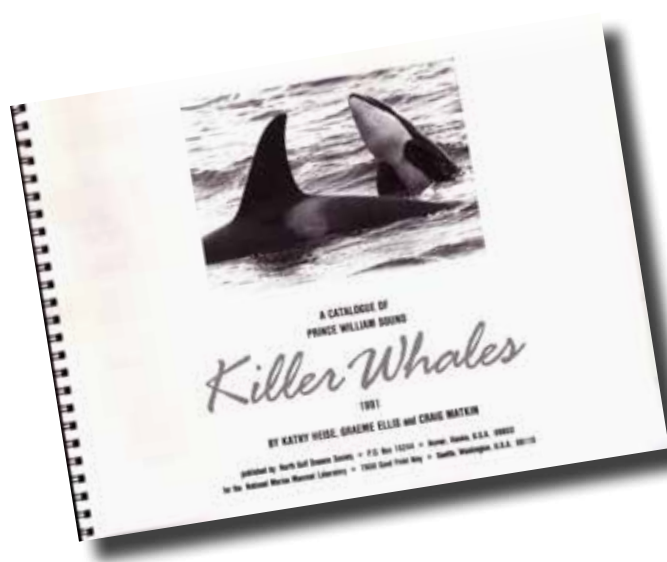
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Author / Urheber :

Craig Matkin

Photo-Identification Catalog / Foto-Identifikationskatalog:

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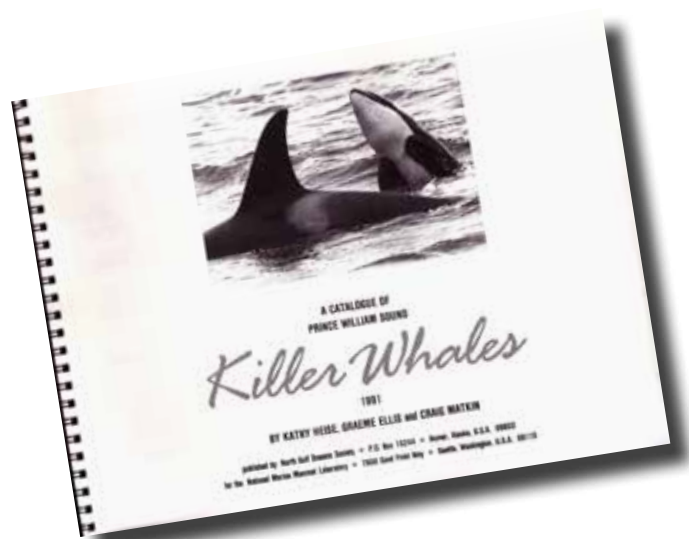
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Date / Datum:
4 August 1986 / 4 de agosto de 1986

Author / Urheber:
Craig Matkin

Photo-Identification Catalog / Foto-Identifikationskatalog

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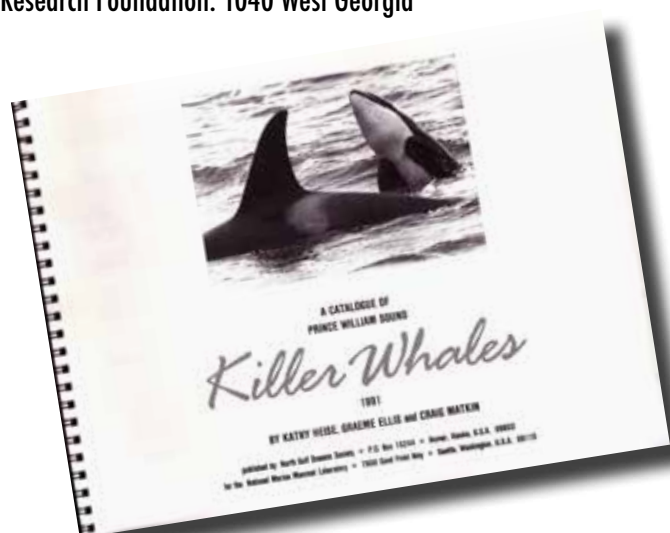


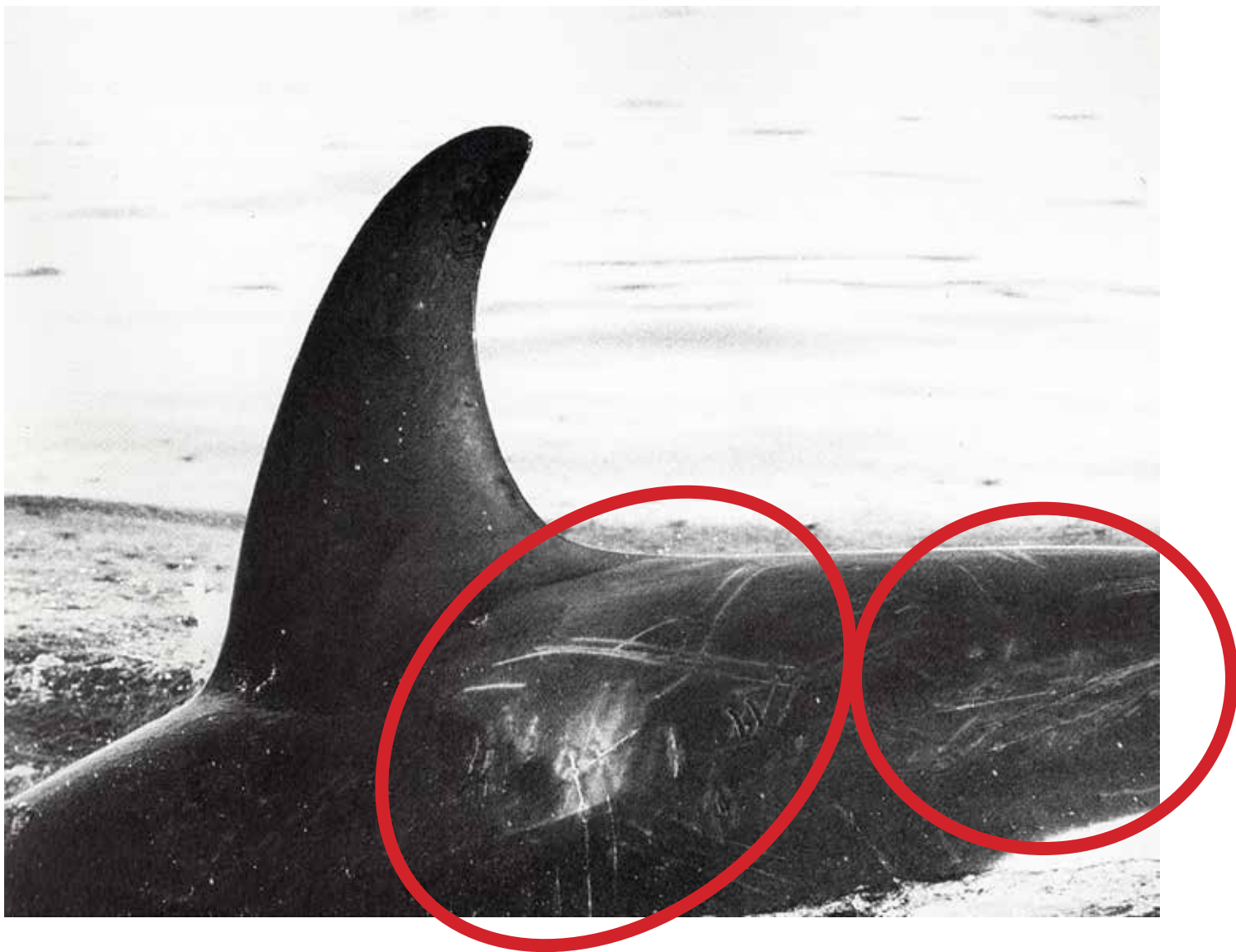
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Date / Datum:
28 August 1984 / 28 de agosto de 1984

Author /Urheber:
Suzanne Healy

Photo-Identification Catalog / Foto-Identifikationskatalog:
Killer whales of Prince William Sound and Southeast Alaska A Catalogue of Individuals Photoidentified, 1976-1986. Edited By Graeme Ellis. West Coast Whale Research Foundation. 1040 West Georgia Street, Room 2020. Vancouver, British Columbia.



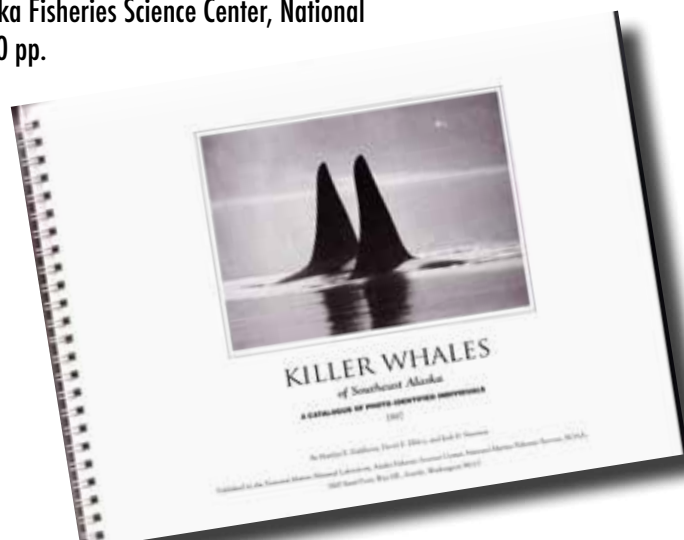


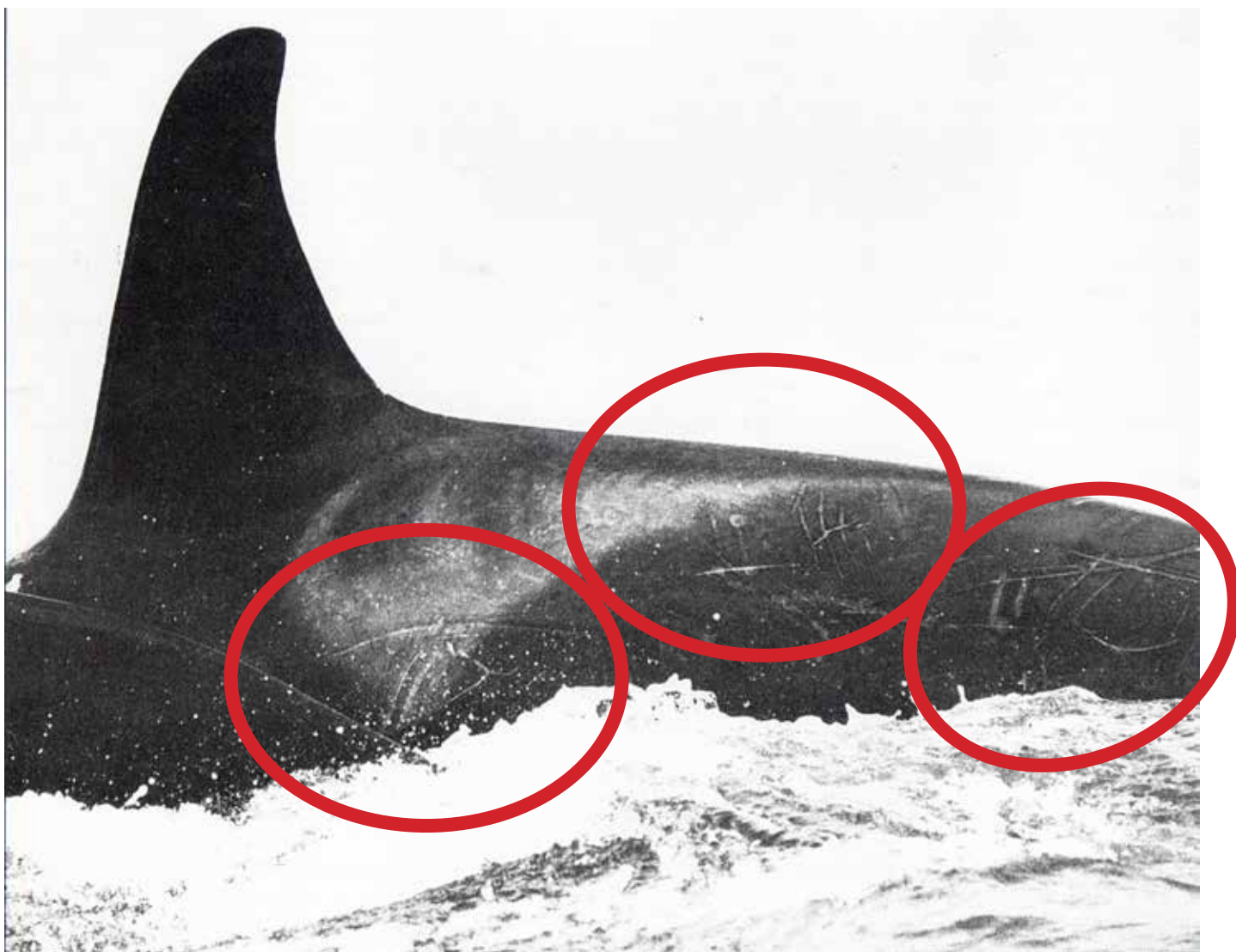
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Killer whales of Southeast Alaska A Catalogue of Photoidentified individuals (1997) Dahlheim, M, Ellifrit D. and Swenson J. Eds. Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service NOAA. Day Moon Press, Washington, 90 pp.



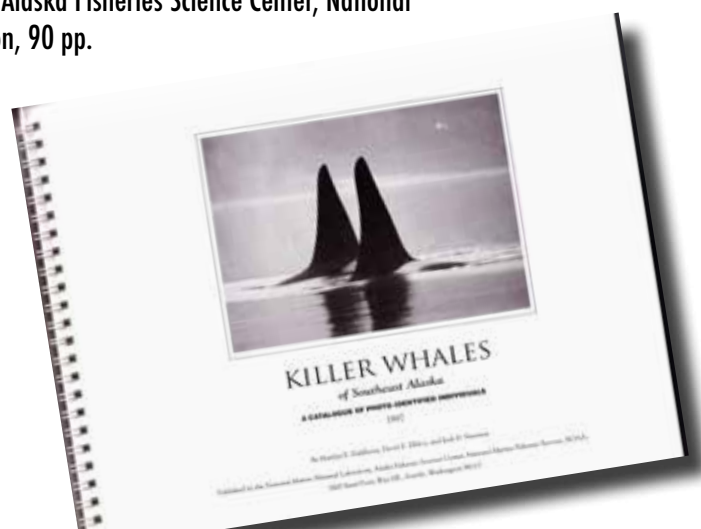


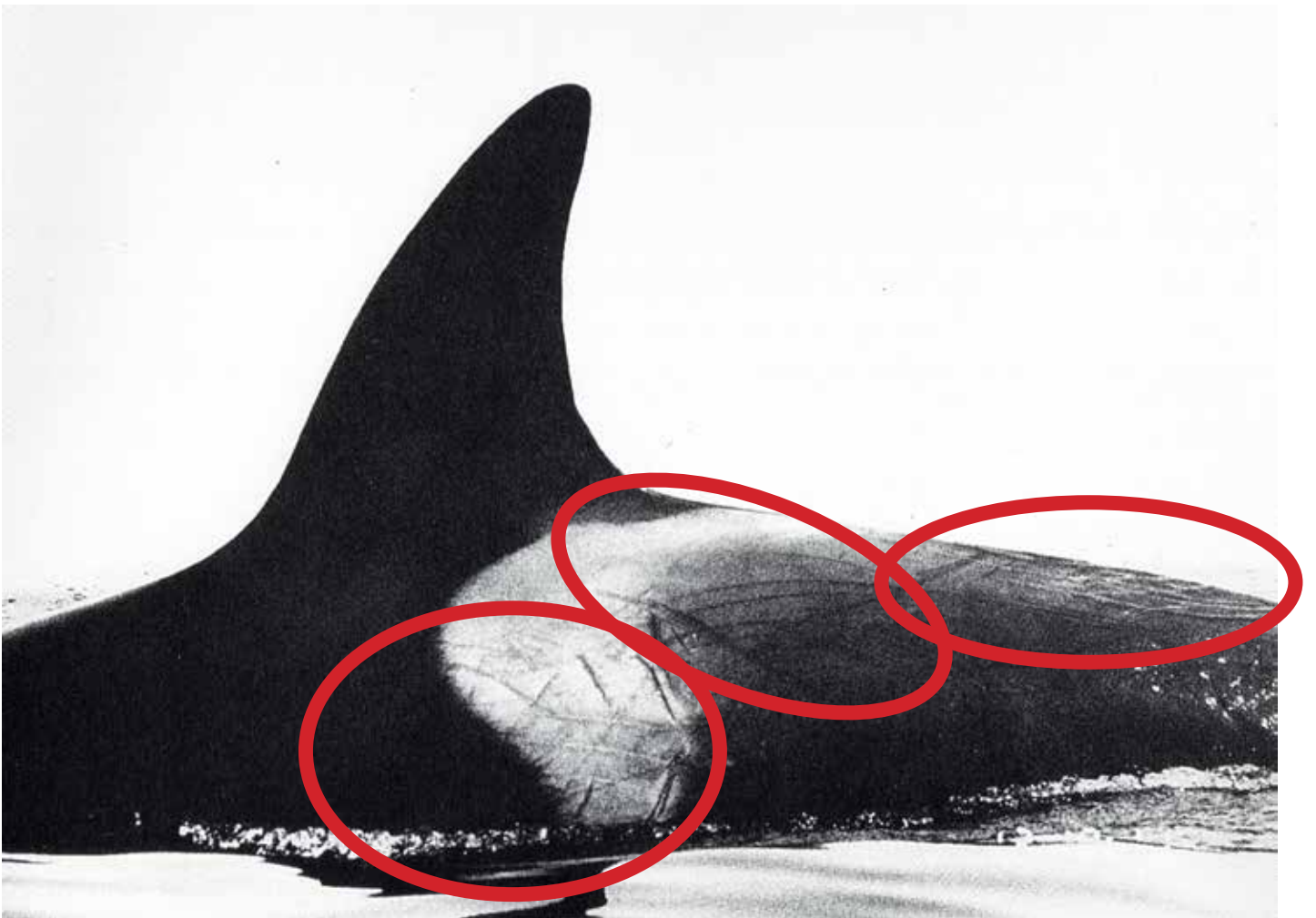
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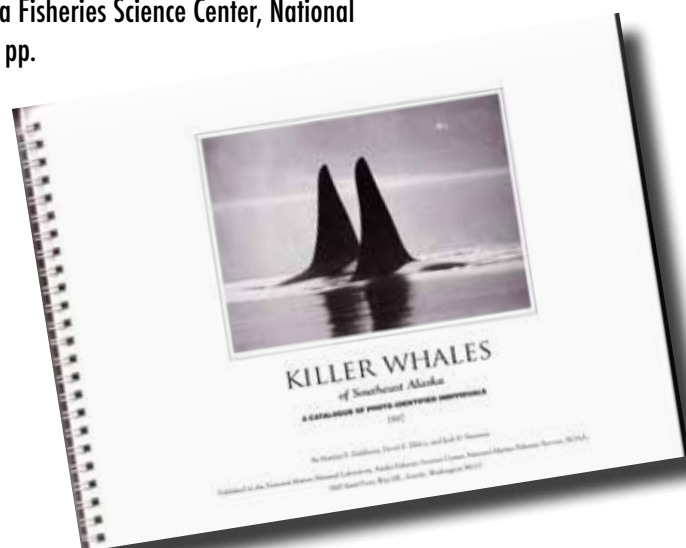


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Date / Datum:
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Individual / Exemplar:

AI 4

Date / Datum:

11 September 1986 / 11 de septiembre de 1986

Author / Urheber:

* Not indicated in the original publication / No indicado en la publicación original

Photo-Identification Catalog / Foto-Identifikationskatalog:

Killer whales of the Prince William sound and Southeast Alaska a catalog of individuals photoidentified, 1976-1986. Sea World Research Institute, Hubbs Marine Research Center. Technical Report N° 87-200. April 1987





Individual / Exemplar:

AJ 10

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Individual / Exemplar:
AJ 15

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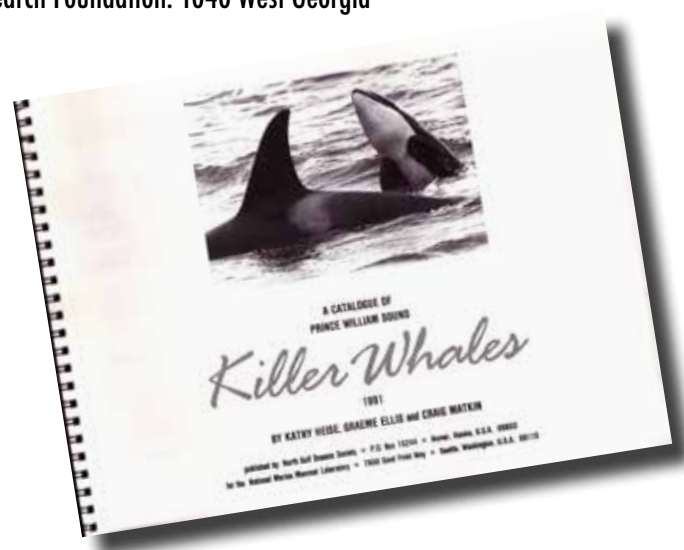
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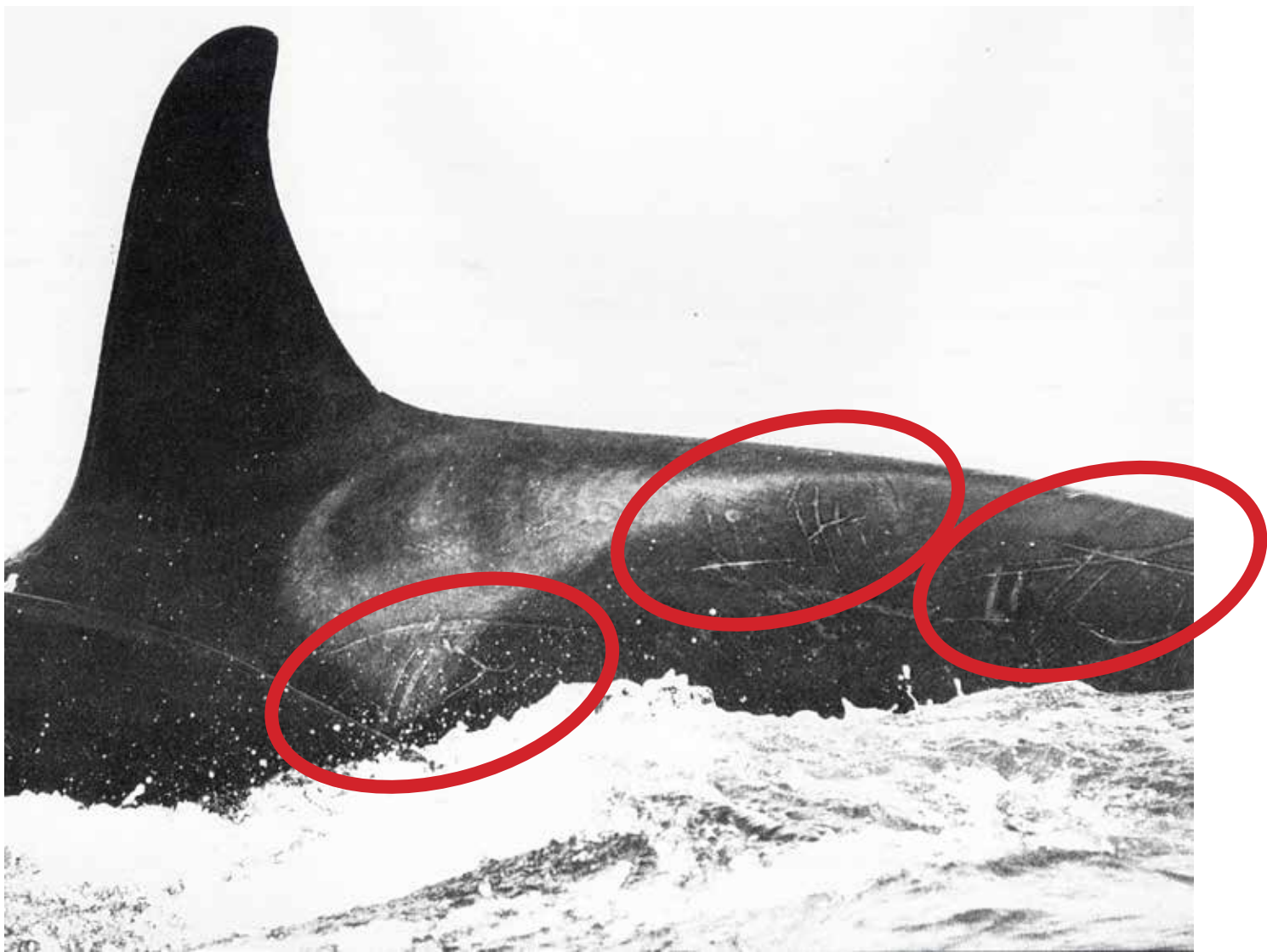
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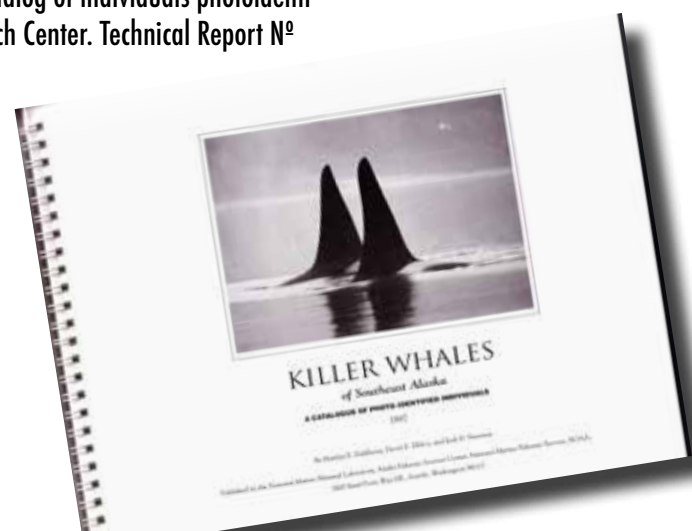
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Date / Datum:
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Author / Urheber:
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Photo-Identification Catalog / Foto-Identifikationskatalog:

Killer whales of the Prince William sound and Southeast Alaska a catalog of individuals photoidentified, 1976-1986. Sea World Research Institute, Hubbs Marine Research Center. Technical Report N° 87-200. April 1987





Individual / Exemplar:
L 88 (Wave walker)

Date / Datum:
16 July 2009 / 16 de Julio de 2009

Author / Urheber:
Dave Ellifrit, Center for Whale Research

Source / Quelle:
<http://pugetsoundblogs.com/waterways/2009/07/16/tooth-marks-on-an-adult-orca-may-spell-minor-conflict/>





Individual / Exemplar:
A 89 (Kanish)

Date / Datum:
24 July 2015

Author / Urheber:
CREXCURSIONS

Source / Quelle
<http://northernresidentorcas.tumblr.com/image/124926887851>





Individual / Exemplar:

*

Date / Datum:

*

Author / Urheber:

Orca Research Trust

Source / Quelle

<http://www.orcaresearch.org/index.php/research/our-team>





Tooth wear / Zahnverschleiß

2.1 Introduction / Einleitung

2.2 Scientific description of tooth abrasion in wild killer whales Wissenschaftliche Darstellung von Zahnabrieb bei wilden Schwertwalen

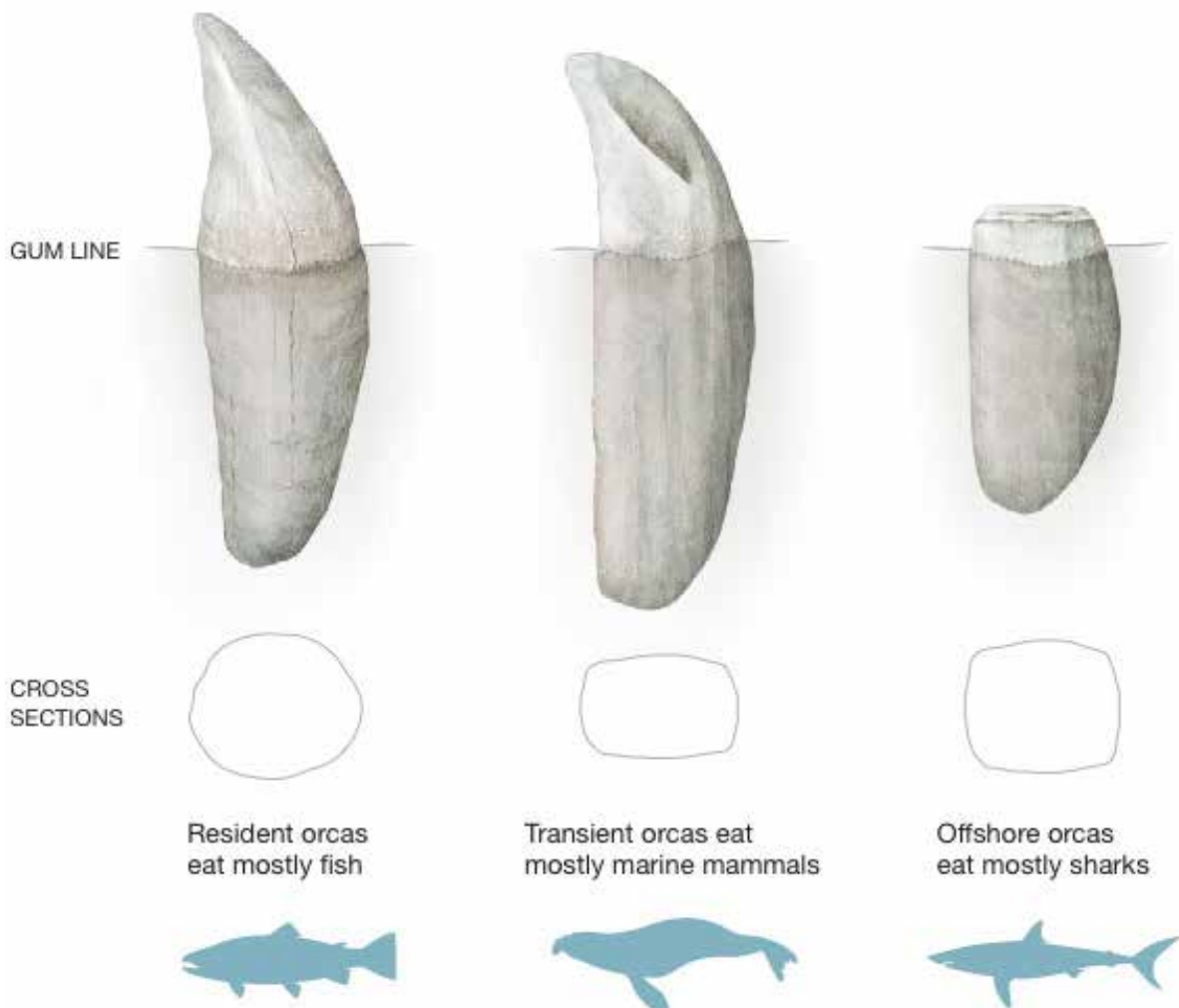
2.3 Some examples of tooth wear in wild orcas from strandings Einige Beispiele von Zahnverschleiß bei gestrandeten wilden Schwertwalen.

2.1

Introduction / Einleitung

Dental problems (dental abrasion and broken teeth) are not exclusive of captive killer whales. The appearance of killer whales' teeth can vary greatly, depending on different factors. Certain ecotypes eat different types of food that will wear down their teeth in different ways. See this illustration from National Geographic (<http://ngm.nationalgeographic.com/2015/07/orca-feeding/img/teeth-graphic-571x493.jpg>) for examples of what different killer whale teeth look like:

Zahnprobleme (Zahnabrieb und gebrochene Zähne) treten nicht nur ausschließlich bei Schwertwalen in Gefangenschaft auf. In Abhängigkeit von unterschiedlichen Faktoren kann der Zustand und das Aussehen der Zähne erheblich variieren. Da sich die Ernährung von bestimmten Ökotypen unterscheidet, nutzen sich ihre Zähne auch in unterschiedlicher Art und Weise ab. Siehe hierzu die Illustration von National Geographic mit Beispielen, wie unterschiedlich die Zähne von verschiedenen Schwertwalen aussehen. (<http://ngm.nationalgeographic.com/2015/07/orca-feeding/img/teeth-graphic-571x493.jpg>)



Shark predation and tooth wear in a population of northeastern Pacific killer whales

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ABSTRACT: The cosmopolitan killer whale *Orcinus orca* feeds on a wide variety of prey types over its global range, but in at least some regions, genetically distinct and ecologically specialised lineages of killer whales coexist sympatrically. In coastal waters of the northeastern Pacific, 2 such lineages have been well described: the so-called 'residents' prey on teleost fish, especially salmonids and the other ('transients') on marine mammals. A third lineage in this region ('offshores') appears from chemical tracers to be ecologically distinct from residents and transients, but its diet is very poorly known. Here we describe 2 encounters with offshore killer whales during which multiple predation events involving sharks were observed. Using DNA analysis of tissue samples collected from these predation events, we identified the prey species as Pacific sleeper shark *Somniosus pacificus* and determined that a minimum of 16 individuals were consumed over the 2 encounters. This represents the first confirmed prey species of offshore killer whales based on field observations of foraging and the first record of any *Somniosus* species in the prey of *Orcinus*. We also show quantitatively that apical tooth wear is far greater in offshores than in resident and transient killer whales, and propose that such wear is at least in part due to abrasion from dermal denticles embedded in shark skin. Further studies are needed to determine whether offshore killer whales are as specialised ecologically as resident and transient killer whales, and whether sharks play a dominant role in their diet.

KEY WORDS: Ecological specialisation · Foraging strategy · Elasmobranch predation · *Orcinus orca*

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INTRODUCTION

There is growing evidence that ecological adaptation and divergence is an important factor promoting reproductive isolation and speciation in a wide variety of taxa (Schluter 2001, Funk et al. 2006). Killer whales *Orcinus orca*, the oceans' apex predators, present an interesting case in which ecological specialisation has been associated with the divergence of the species into genetically distinct lineages that maintain social and reproductive isolation even in sympatry (Bigg 1982, Barrett-Lennard 2000, Ford et al. 2000, Pitman & Ensor 2003, Foote et al. 2009, Morin et al. 2010). Some have suggested that such genetically and ecologically distinct lineages may be incipient (e.g. Baird et al. 1992)

or separate (e.g. LeDuc et al. 2008, Morin et al. 2010) species.

As the most cosmopolitan of cetaceans, killer whales occur in all marine regions, from high-latitude Arctic and Antarctic waters to the tropics. The species has been documented to feed on more than 140 prey species, including marine mammals (cetaceans, pinnipeds, mustelids, sirenians), birds, turtles, fish (teleosts, elasmobranchs), and invertebrates (cephalopods, tunicates) (Ford 2009). However, culturally-determined foraging specialisations may constrain the diet breadth of lineages to a much narrower range of prey species. The most studied killer whales inhabit temperate coastal waters of the northeastern Pacific, where research on life history, social organisation, behaviour and foraging

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DNA sequences were evaluated and aligned in Sequencher V4.6 (GeneCodes) and MEGA4. The National Center for Biotechnology Information (NCBI) Basic Local Alignment Search Tool (BLAST) was used to search GenBank for highly similar 16S and *cytb* sequences. Sequence analysis was carried out using MEGA4. Percentage sequence divergences or distances (D) were estimated with the Kimura 2 parameter (K2P) distance model (Kimura 1980). Haplotypes were depicted in neighbour-joining (NJ) trees constructed with the 'pairwise deletion of missing nucleotide data' option. Bootstrap support for each branch point was obtained using 500 replicates. The 16S sequences from 3 potential prey species (*Squalus acanthias*, *Hexanchus griseus* and broadnose sevengill shark *Notorhynchus cepedianus*) and *Somniosus rostratus* obtained from GenBank were included in the NJ tree. Mean within- and between-species distances were determined in MEGA4. Standard error estimates were calculated by bootstrapping 500 times.

Analysis of tooth wear. Teeth of stranded killer whales and museum specimens were assessed for extent of apical tooth wear, either by direct visual inspection of museum specimens or from photographs of stranded or living animals. In most cases, population or lineage affiliation of individuals was determined from natural markings (Ford et al. 2000), but in 2 cases this was determined from DNA analysis. In these cases, a bone sample was obtained from the skull by drilling a 5 mm diameter hole several mm deep in the occipital condyle, discarding the shavings and flaming the drill bit to minimise the risk of contamination, and then drilling ~1.5 cm deeper while retaining the shavings on sterilised foil. The shavings were then digested in Proteinase K for 24 h at 54°C under gentle rotation. DNA was purified from this solution with phenol and chloroform and precipitated with ethanol, then dried and eluted in 100 µl TE buffer following Sambrook et al. (1989). A 262 bp region of the mtDNA CR was amplified using the custom-designed primers LBDL1 (5' TAA ATA ACA CCT GTT GGT TGT G 3') and LBDL3 (5' CAT CTG GTT CTT ACT TCA GGA C 3'). PCR reaction solutions of 25 µl were prepared using 1 unit of *Taq* polymerase (New England Biolabs), 1× PCR reaction buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 0.01% gelatin, 3 µg BSA), 3 mM dNTPs, 1.5 mM MgCl₂ and 20 pmol of each primer. The PCR thermal profile was 3 min at 94°C, 31 cycles of 94°C for 50 s, 61°C for 1 min, and 72°C for 3 min, followed by 1 cycle of 72°C for 25 min. DNA sequencing was performed in both directions as described by Matkin et al. (2007).

Forward and reverse sequences were manually checked and aligned with sequences for biopsy-sampled northeastern Pacific killer whales determined by Barrett-Lennard (2000), who described variable

sites in the amplified region defining a single haplotype unique to all 7 known offshore killer whales in his dataset. Furthermore, of these 5 sites, 1 distinguished offshores from 119 residents and transients from the northeastern Pacific and from 4 killer whales of unknown population identity from the Atlantic. Here, identification of offshores was considered positive if the diagnostic site as determined in both the forward and reverse sequences matched the site in Barrett-Lennard's (2000) offshores, and if at least 2 of the other informative sites were clearly resolved and also consistent with Barrett-Lennard's (2000) offshore haplotype.

The degree of apical wear on the crowns of teeth was rated on a scale of 0 (negligible) to 4 (extreme) as described in Table 1. Apical wear was categorised based on the degree of flattening of the tooth crown expressed as a percentage of the tooth diameter at the gum line. In museum specimens, this could be measured directly, but in photos of stranded or living individuals, the rating of tooth wear was estimated.

RESULTS

Field observations of predation

During 2 encounters with offshore killer whales, multiple predation events were documented by the collection of tissue fragments from consumed prey. Details of these encounters are as follows:

30 May 2008

A group of 5 offshore killer whales was observed over a period of 8.6 h at Learmonth Bank, western Dixon Entrance, British Columbia (54° 19' N, 132° 56' W) on 30 May 2008. When first encountered at 10:23 h, the whales appeared to be actively foraging. They swam rapidly with frequent changes in direction, and acoustic monitoring revealed considerable vocal activity. Series of short, apparently shallow dives were followed by

Table 1. *Orcinus orca*. Categories of apical tooth wear

Category	Wear	Crown worn to
0	Negligible	<10% of diameter of tooth at gum line
1	Minor	10–25% of tooth diameter
2	Moderate	25–50% of tooth diameter
3	Major	50–75% of tooth diameter
4	Extreme	75–100% of tooth diameter, exposed pulp cavities in some or most teeth

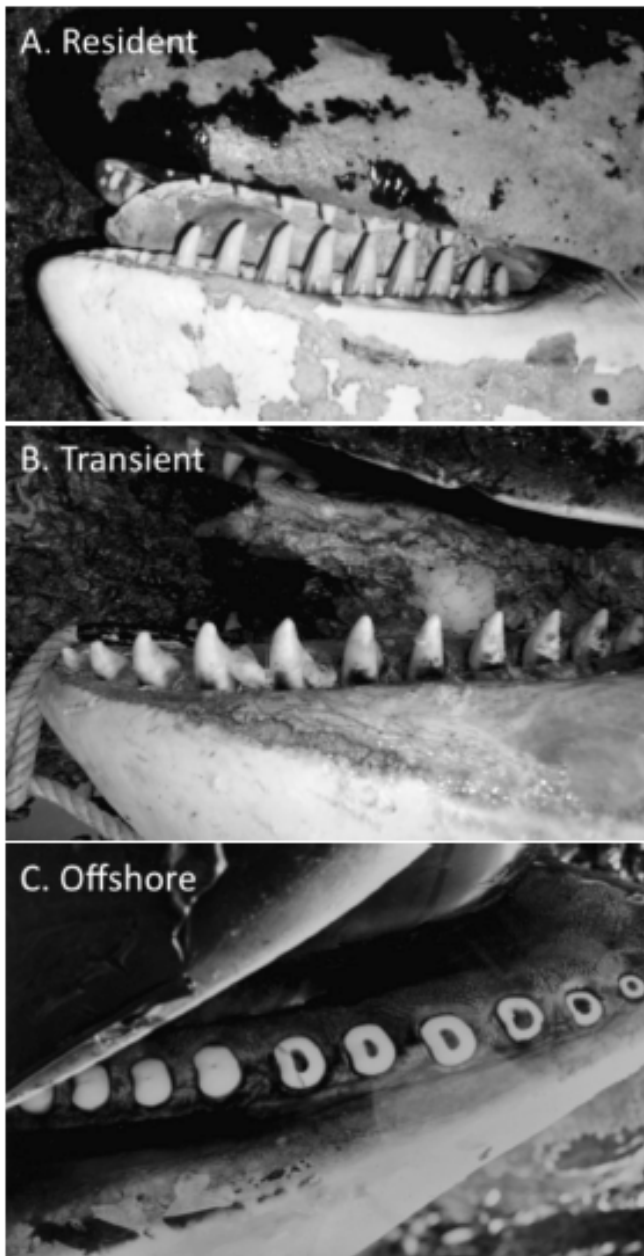


Fig. 3. *Orcinus orca*. Representative photographs of killer whale teeth: (A) resident female A9, (B) transient male T44 and (C) offshore female O120 (all adults). Photo (C) by R. Palm

median daily depth range of 184 m (range of daily medians = 116 to 254 m, Hulbert et al. 2006). These depths are similar to those at the locations of *Somniosus pacificus* predation observed here, and are within the maximum dive depths observed in piscivorous resident killer whales (Baird et al. 2005; J. Ford & G. Ellis unpubl. data).

Like most deep water sharks, *Somniosus* have a very large liver that is rich in lipids (up to 80% by weight), which appears to serve in buoyancy control at depth (Phleger 1998). A 3.93 m Pacific sleeper shark esti-

mated to weigh ~900 kg had a liver of ~180 kg (Bright 1959), or ~20% of its total mass. Thus, a median sized 1.7 m sleeper shark (Hulbert et al. 2006) having a mass of 75 kg (L. Hulbert pers. comm.) would have a liver of ~15 kg. Given the high lipid content of shark liver, this represents a substantial, high energy food source for a killer whale.

Piscivorous killer whales appear to select prey at least partly on the basis of size and lipid content. Resident killer whales forage selectively for Chinook salmon, which is the largest and most lipid rich of the Pacific salmon species (Ford & Ellis 2006), and killer whales that take fish from longline fishing gear tend to select the largest individuals of lipid-rich species and shun smaller or lipid-poor species (Matkin & Saulitis 1994, Yano & Dahlheim 1995). Although offshore killer whales were observed to retrieve and presumably feed on pieces of sleeper shark liver, it is not known if other parts of the shark flesh were eaten. The whales may have fed selectively on the liver because it seems unlikely that 5 killer whales would consume the flesh of 11 sleeper sharks in a single day (30 May 2008), given the median size of the sharks observed in Alaska (1.7 m, 75 kg). Pyle et al. (1999) observed 2 killer whales preying on a 3 to 4 m long white shark *Carcharodon carcharias* and noted that only the liver was consumed. Mammal-hunting killer whales often strip porpoises of their blubber and discard the remainder of the carcass (J. Ford, G. Ellis, L. Barrett-Lennard unpubl. data). Furthermore, the musculature of the congeneric Greenland sleeper shark *Somniosus microcephalus* contains high levels of trimethylamine and is poisonous to humans and dogs (Bagnis et al. 1970, Anthoni et al. 1991). *S. pacificus* muscle may be similarly toxic, possibly to whales as well.

Although the foraging activities of offshore killer whales on the 2 occasions described here appeared to be focused on Pacific sleeper sharks, the importance of sharks in the diet of this lineage is unclear. However, the stomach contents collected from known offshores (blue or whitetip shark, opah, and halibut; Rice 1968, Morin et al. 2006, this study) suggest that sharks and large teleost fish may be important. This is consistent with the findings of Krahn et al. (2007), who concluded from analyses of fatty acids, stable isotopes and persistent organic pollutant (POP) levels that the diet of offshore killer whales likely consists of long-lived, high trophic level marine fishes.

The tooth wear of offshore killer whales provides further evidence that their diet is distinct from that of resident or transient killer whales. The **teeth** of offshore killer whales we examined had severe apical wear; the mandibular teeth were often worn to the gum line and exhibited exposed pulp cavities. In contrast, apical tooth wear in adult resident and transient killer whales

The following supplement accompanies the article

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Aquatic Biology 11: 213–224 (2011)

Offshore 1997-08-29, ID 0120



Resident, 1999-09-26, ID L51



2.3

Some examples of tooth wear in wild orcas from strandings

Einige Beispiele von Zahnverschleiß bei gestrandeten wilden Schwertwalen



Scottish Marine Animal Stranding Scheme ASIMETRIC Tooth wear in an stranded suction feeder killer whale.

Abrasión dental asimétrica en una orca varada de un ecotipo que se alimenta por succión.
Scottish Marine Animal stranding scheme.

Example of tooth wear in a stranded killer whale in Port Moller (Alaska)

Beispiel der Abnutzung von Zähnen bei einem gestrandeten Orca in Port Moller (Alaska)

MARINE MAMMAL STRANDING REPORT - LEVEL A DATA

FIELD #: 2013 NMFS REGIONAL #: 2013186 NATIONAL DATABASE#: _____
(NMFS USE) (NMFS USE)

COMMON NAME: killer whale GENUS: Orcinus SPECIES: orca

EXAMINER Name: Aleria Jensen Affiliation: NMFS

Address: _____ Phone: _____

Stranding Agreement or Authority: 109h

LOCATION OF INITIAL OBSERVATION State: <u>AK</u> County: _____ City: <u>Port Moller</u> Body of Water: <u>Bristol Bay</u> Locality Details: _____ Lat (DD): _____ N Long (DD): _____ W <input type="checkbox"/> Actual <input type="checkbox"/> Estimated How Determined: (check ONE) <input type="checkbox"/> GPS <input type="checkbox"/> Map <input type="checkbox"/> Internet/Software	OCURRENCE DETAILS <input type="checkbox"/> Restrand GE# _____ Group Event: <input type="checkbox"/> YES <input type="checkbox"/> NO (NMFS Use) If Yes, Type: <input type="checkbox"/> Cow/Calf Pair <input type="checkbox"/> Mass Stranding # Animals: _____ <input type="checkbox"/> Actual <input type="checkbox"/> Estimated Findings of Human Interaction: <input type="checkbox"/> YES <input type="checkbox"/> NO <input type="checkbox"/> Could Not Be Determined (CBD) If Yes, Choose one or more: <input type="checkbox"/> 1. Boat Collision <input type="checkbox"/> 2. Shot <input type="checkbox"/> 3. Fishery Interaction <input type="checkbox"/> 4. Other Human Interaction: _____ How Determined (Check one or more): <input type="checkbox"/> External Exam <input type="checkbox"/> Internal Exam <input type="checkbox"/> Necropsy <input type="checkbox"/> Other: _____ Gear Collected? <input type="checkbox"/> YES <input type="checkbox"/> NO Gear Disposition: _____ Other Findings Upon Level A: <input type="checkbox"/> YES <input type="checkbox"/> NO <input type="checkbox"/> Could Not Be Determined (CBD) If Yes, Choose one or more: <input type="checkbox"/> 1. Illness <input type="checkbox"/> 2. Injury <input type="checkbox"/> 3. Pregnant <input type="checkbox"/> 4. Other: _____ How Determined (Check one or more): <input type="checkbox"/> External Exam <input type="checkbox"/> Internal Exam <input type="checkbox"/> Necropsy <input type="checkbox"/> Other: _____																																										
INITIAL OBSERVATION Date: Year: <u>2013</u> Month: <u>November</u> Day: <u>4</u> First Observed: <input type="checkbox"/> Beach or Land <input type="checkbox"/> Floating <input type="checkbox"/> Swimming CONDITION AT INITIAL OBSERVATION (Check ONE) <input type="checkbox"/> 1. Alive <input type="checkbox"/> 4. Advanced Decomposition <input type="checkbox"/> 2. Fresh dead <input type="checkbox"/> 5. Mummified/Skeletal <input type="checkbox"/> 3. Moderate decomposition <input type="checkbox"/> 6. Condition Unknown	LEVEL A EXAMINATION <input type="checkbox"/> Not Able to Examine Date: Year: _____ Month: _____ Day: _____ CONDITION AT EXAMINATION (Check ONE) <input type="checkbox"/> 1. Alive <input type="checkbox"/> 4. Advanced Decomposition <input type="checkbox"/> 2. Fresh dead <input type="checkbox"/> 5. Mummified/Skeletal <input type="checkbox"/> 3. Moderate decomposition <input type="checkbox"/> 6. Unknown																																										
INITIAL LIVE ANIMAL DISPOSITION (Check one or more) <input type="checkbox"/> 1. Left at Site <input type="checkbox"/> 6. Euthanized at Site <input type="checkbox"/> 2. Immediate Release at Site <input type="checkbox"/> 7. Transferred to Rehabilitation: Date: Year: _____ Month: _____ Day: _____ Facility: _____ <input type="checkbox"/> 3. Relocated <input type="checkbox"/> 8. Died during Transport <input type="checkbox"/> 4. Disentangled <input type="checkbox"/> 9. Euthanized during Transport <input type="checkbox"/> 5. Died at Site <input type="checkbox"/> 10. Other: _____	MORPHOLOGICAL DATA SEX (Check ONE) AGE CLASS (Check ONE) <input type="checkbox"/> 1. Male <input type="checkbox"/> 1. Adult <input type="checkbox"/> 4. Pup/Calf <input type="checkbox"/> 2. Female <input type="checkbox"/> 2. Subadult <input type="checkbox"/> 5. Unknown <input type="checkbox"/> 3. Unknown <input type="checkbox"/> 3. Yearling <input type="checkbox"/> Whole Carcass <input type="checkbox"/> Partial Carcass Straight length: <u>222</u> cm <input type="checkbox"/> in <input type="checkbox"/> actual <input type="checkbox"/> estimated Weight: <u>n/a</u> kg <input type="checkbox"/> lb <input type="checkbox"/> actual <input type="checkbox"/> estimated PHOTOS/VIDEOS TAKEN: <input type="checkbox"/> YES <input type="checkbox"/> NO Photo/Video Disposition: _____ photos sent by observer _____																																										
CONDITION/DETERMINATION (Check one or more) <input type="checkbox"/> 1. Sick <input type="checkbox"/> 7. Location Hazardous <input type="checkbox"/> 2. Injured <input type="checkbox"/> a. To animal <input type="checkbox"/> 3. Out of Habitat <input type="checkbox"/> b. To public <input type="checkbox"/> 4. Deemed Releasable <input type="checkbox"/> 8. Unknown/CBD <input type="checkbox"/> 5. Abandoned/Orphaned <input type="checkbox"/> 9. Other: _____ <input type="checkbox"/> 6. Inaccessible	CARCASS STATUS (Check one or more) <input type="checkbox"/> 1. Left at Site <input type="checkbox"/> 4. Towed: Lat _____ Long _____ <input type="checkbox"/> 7. Landfill <input type="checkbox"/> 2. Buried <input type="checkbox"/> 5. Sunk: Lat _____ Long _____ <input type="checkbox"/> 8. Unknown <input type="checkbox"/> 3. Rendered <input type="checkbox"/> 6. Frozen for Later Examination <input type="checkbox"/> 9. Other: _____ SPECIMEN DISPOSITION (Check one or more) <input type="checkbox"/> 1. Scientific collection <input type="checkbox"/> 2. Educational collection <input type="checkbox"/> 3. Other: _____ Comments: <u>see remarks section</u> NECROPSIED <input type="checkbox"/> NO <input type="checkbox"/> YES <input type="checkbox"/> Limited <input type="checkbox"/> Complete <input type="checkbox"/> Carcass Fresh <input type="checkbox"/> Carcass Frozen/Thawed NECROPSIED BY: _____ Date: Year: _____ Month: _____ Day: _____																																										
TAG DATA Tags Were: Present at Time of Stranding (Pre-existing): <input type="checkbox"/> YES <input type="checkbox"/> NO Applied during Stranding Response: <input type="checkbox"/> YES <input type="checkbox"/> NO <table border="1" style="width: 100%; border-collapse: collapse; margin-top: 5px;"> <thead> <tr> <th>ID#</th> <th>Color</th> <th>Type</th> <th>Placement* (Circle ONE)</th> <th>Applied</th> <th>Present</th> </tr> </thead> <tbody> <tr> <td></td> <td></td> <td></td> <td>D DF L</td> <td><input type="checkbox"/></td> <td><input type="checkbox"/></td> </tr> <tr> <td></td> <td></td> <td></td> <td>LF LR RF RR</td> <td><input type="checkbox"/></td> <td><input type="checkbox"/></td> </tr> <tr> <td></td> <td></td> <td></td> <td>D DF L</td> <td><input type="checkbox"/></td> <td><input type="checkbox"/></td> </tr> <tr> <td></td> <td></td> <td></td> <td>LF LR RF RR</td> <td><input type="checkbox"/></td> <td><input type="checkbox"/></td> </tr> <tr> <td></td> <td></td> <td></td> <td>D DF L</td> <td><input type="checkbox"/></td> <td><input type="checkbox"/></td> </tr> <tr> <td></td> <td></td> <td></td> <td>LF LR RF RR</td> <td><input type="checkbox"/></td> <td><input type="checkbox"/></td> </tr> </tbody> </table> <p>* D= Dorsal; DF= Dorsal Fin; L= Lateral Body LF= Left Front; LR= Left Rear; RF= Right Front; RR= Right Rear</p>		ID#	Color	Type	Placement* (Circle ONE)	Applied	Present				D DF L	<input type="checkbox"/>	<input type="checkbox"/>				LF LR RF RR	<input type="checkbox"/>	<input type="checkbox"/>				D DF L	<input type="checkbox"/>	<input type="checkbox"/>				LF LR RF RR	<input type="checkbox"/>	<input type="checkbox"/>				D DF L	<input type="checkbox"/>	<input type="checkbox"/>				LF LR RF RR	<input type="checkbox"/>	<input type="checkbox"/>
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Example of tooth wear in a stranded killer whale in Port Moller (Alaska)

Beispiel der Abnutzung von Zähnen bei einem gestrandeten Orca in Port Moller (Alaska)

ADDITIONAL REMARKS

ADDITIONAL IDENTIFIER: _____ (If animal is restranded, please indicate any previous field numbers here)

On 11/6/13, NMFS Alaska Marine Mammal Stranding Program received a call about two stranded dead killer whales in Port Moller. The whales were first spotted 4 mi apart on 11/4/13 and are believed by locals to have washed ashore during a recent storm. Given the unusual nature of the event and the high priority of responding to killer whales, stranding network member organizations worked on logistics to attempt necropsy, but ultimately on-site response proved too challenging to pursue (lack of flights, personnel limitations, cost). Instead, local caretaker at Port Moller Dennis Tinker was able to collect tissues from each animal and send to Kathy Burek AVPS for analysis and distribution. Bears were seen on each carcass soon after sample collection.

The following tissues were collected:

skin
blubber
tongue
lower jaw chunk with teeth in the jaw

Also length, dorsal fin & tail measurements as follows:

Information for Killer Whale #2 - PortMoller/Franks Lagoon

- (1) Total length - 22'
- (29) Flipper length - 33"
- (30) Flipper length - 24"
- (31) Maximum width of flipper - 18"
- (32) Height of dorsal fin - 21"
- (33) Length of dorsal fin - 22"
- (34) Width of flukes - 5'





Killer whale skull at the Oxford University Museum of Natural History
 Schwertwalschädel im Naturkundemuseum der Oxford University



Skull of a young killer whale stranded at Ras Marbat in June, 1989. Oman National History Museum, Whale Pavillion
 (Killer whales are rarely reported near Oman.)
 Schädel eines jungen Schwertwals, der im Juni 1989 bei Ras Marbat strandete. Naturkundemuseum Oman, Walpavillon
 (Schwertwale werden sehr selten in der Nähe des Oman gesichtet)



Skeleton of "Old Tom" in the Eden Killer Whale Museum. On this side you can see where Tom's teeth are worn down to the nub through grabbing the whaling boats' ropes to pull them along

Skelett von „Old Tom“ im Schwertwalmuseum von Eden. Auf dieser Seite kann man sehen, dass Toms Zähne durch das Greifen der Seile um die Walfangboote umherzuziehen, fast komplett abgenutzt sind.



Orca teeth; Credit: © Proceedings of the Royal Society B: Biological Sciences - See more at: <http://www.earthtimes.org/scitech/niches-speciation-orca/2419/#sthash.fjd1KhT9.dpuf>

Schwertwalzähne; Anerkennung: © Das Vorgehen der Königlichen Gesellschaft (Royal Society) B: Biowissenschaften – Siehe auch: <http://www.earthtimes.org/scitech/niches-speciation-orca/2419/#sthash.fjd1KhT9.dpuf>



Tear film / Tränenflüssigkeit

3.1 Veterinary statement about tear film in killer whales Tiermedizinische Stellungnahme zum Tränenflüssigkeit bei Schwertwalen

3.1

Veterinary statement about tear film in killer whales Tiermedizinische Stellungnahme zum Tränenflüssigkeit bei Schwertwalen



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geraldine.lacave@icloud.com - BTW: BE 0519 844 675

VETERINARY STATEMENT ABOUT TEAR FILM IN KILLER WHALES

To whom this may concern,

As an independent veterinarian specialized in marine mammals for 25 years, I am also consulting at Loro Parque, where a population of 6 killer whales is residing.

I have been asked to make a statement on the heavy mucous appearance of the tear film of the whales in that facility.

Tears provide oxygen and nutrients to the avascular cornea and remove metabolic wastes from the surface, working as a natural barrier and protection to the environment.

An innermost mucin and outermost aqueous layers form the tear film layers in marine mammals (they do lack the lipid layer found in terrestrial animals). Cetaceans have no eye lashes and the production of mucin in the tear film is massive

They have a basal tear secretion, which is a continuous tear production (with a thick appearance) that is not related to any stimulation.

As such, the presence of tears with a seromucous appearance around the eyes of these animals is a complete normal phenomenon.

Dr. Geraldine Lacave
Marine Mammal Veterinary Services
Brugge, Belgium
(26 Aug 2015)



Life expectancy / Lebenserwartung

4.1 Introduction / Einleitung

4.2 Scientific literature on killer whale life expectancy

Wissenschaftliche Literatur zur Lebenserwartung von Schwertwalen.

4.1

Introduction / Einleitung

The first determination of the life expectancy for *Orcinus orca* was published almost 25 years ago, using age-based mortality rates calculated from observations of the Southern and Northern resident killer whales off Washington State. In that study the mean life expectancy of the species was determined to be 50 years for the females and 30 years for the males. These calculations, and the associated maximum longevity estimations (80 years for females and 60 for the males) have been widely used and accepted since then. These data included many individuals with estimated ages that were affecting the precision of the results.

A current review of the ages of the killer whales living in the coast of Washington State reveals that post-reproductive females are less abundant than predicted by the model published in 1990. A recent scientific research comparing free-ranging and captive killer whale populations evidence similar life-history parameters. That research proves that Killer whale life expectancy was overestimated by previous research, and also proves that the longevity of free-ranging and captive killer whales is similar. (See 4.2). The results of this study give an estimation on mean life expectancy for killer whales of:

Eastern-North Pacific Southern Residents (SR): 20,1 (male) and 29,0 (female)

Eastern-North Pacific Northern Residents (NR): 29 (male) and 42 (female)

SEA (SeaWorld whole population): 28,8 (male) and 41,6 (female)

SEA (SeaWorld considering only captive bred): 33,1 (male) and 47,7 (female)

Die erste Bestimmung der Lebenserwartung von *Orcinus Orca* wurde vor fast 25 Jahren veröffentlicht. Dabei wurden altersbedingte Sterblichkeitsraten verwendet, die auf Grund von Beobachtungen der südlichen und nördlichen residenten Schwertwale des US-Bundesstaates Washington ermittelt wurden. Bei der Studie wurde bestimmt, dass die mittlere Lebenserwartung bei Weibchen 50 Jahre beträgt und bei Männchen 30 Jahre. Diese Berechnungen und die daraus abgeleiteten Schätzungen der maximalen Lebensdauer (80 Jahre bei Weibchen und 60 bei Männchen) wurden seitdem auch weitestgehend verwendet und akzeptiert. Diese Daten bezogen viele Individuen mit ein deren Alter lediglich geschätzt werden konnte, was die Genauigkeit der Ergebnisse beeinträchtigte.

Ein aktueller Bericht über das Alter von Schwertwalen, die an der Küste des US-Bundesstaates Washington leben, zeigt, dass es bei weitem weniger Schwertwalweibchen jenseits des fortpflanzungsfähigen Alters gibt, als es von dem 1990 veröffentlichten Modell vorausgesagt wurde. Eine kürzlich erstellte wissenschaftliche Studie, die wild lebende und in Gefangenschaft lebende Schwertwale vergleicht, liefert Beweise für gleiche Parameter ihrer Lebenszyklen. Diese Forschungsarbeit belegt, dass die Lebenserwartung bei Schwertwalen von früheren Studien überschätzt wurde und dass die Lebensdauer von frei lebenden und in Gefangenschaft lebenden Schwertwalen ähnlich ist. (siehe 4.2) Die Ergebnisse dieser Studie ergeben eine Schätzung für die mittlere Lebenserwartung der Schwertwale:

Im Nordostpazifik, im südlichen Teil ansässige Schwertwale (SR): 20,1 (Männchen) und 29,0 (Weibchen)

Im Nordostpazifik, im nördlichen Teil ansässige Schwertwale (NR): 29 (Männchen) und 42 (Weibchen)

Von SEA (SeaWorlds komplette Population): 28,8 (Männchen) und 41,6 (Weibchen)

Von SEA (nur Schwertwale bei SeaWorld, die in Gefangenschaft geboren wurden): 33,1 (Männchen) und 47,7 (Weibchen)



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Comparisons of life-history parameters between free-ranging and captive killer whale (*Orcinus orca*) populations for application toward species management

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Data collected on life-history parameters of known-age animals from the northern (NR) and southern resident (SR) killer whales (*Orcinus orca*) of the eastern North Pacific were compared with life-history traits of killer whales located at SeaWorld (SEA) facilities. For captive-born SEA animals, mean age and body length at 1st estrus was 7.5 years and 483.7 cm, respectively. Estimated mean age at 1st conception was different ($P < 0.001$) for the combined data from both northern and southern resident (NSR) free-ranging populations (12.1 years) compared to SEA (9.8 years), as was the estimated mean age at 1st observed calf (SEA: 11.1 years, NSR: 14.2 years, $P < 0.001$). Average calf survival rate to 2 years of age for SEA animals (0.966) was significantly greater ($P = 0.04$) than that for SR (0.799). Annual survival rate (ASR) for SEA increased over approximately 15-year increments with rates in the most recent period (2000–2015 ASR: 0.976) improved ($P < 0.05$) over the first 2 periods of captivity (1965–1985: 0.906; 1985–2000: 0.941). The SR (0.966) and NR ASR (0.977) were higher ($P \leq 0.05$) than that of SEA until 2000, after which there were no inter-population differences. Based on ASR, median and average life expectancy were 28.8 and 41.6 years (SEA: 2000–2015), 20.1 and 29.0 years (SR), and 29.3 and 42.3 years (NR), respectively. The ASR for animals born at SEA (0.979) was higher ($P = 0.02$) than that of wild-caught SEA animals (0.944) with a median and average life expectancy of 33.1 and 47.7 years, respectively. These data present evidence for similar life-history parameters of free-ranging and captive killer whale populations and the reproductive potential and survivorship patterns established herein have application for use in future research concerning the overall health of both populations.

Key words: fecundity, gestation, longevity, mortality, orca, reproductive maturity, survivorship

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With estimated worldwide population levels at a minimum of 50,000 (Taylor et al. 2013), killer whales (*Orcinus orca*) are considered one of the most ubiquitous top predators in the oceans, occurring in most of the available habitats (Dahlheim and Heyning 1999). Although there is consensus that specialized killer whale lineages or ecotypes exist, the degree of genetic and/or reproductive isolation between or within these ecotypes is under debate (Barrett-Lennard et al. 2001; Riesch et al. 2012; de Bruyn et al. 2013). The killer whale populations in the eastern North Pacific Ocean are by far the most studied and best understood. Three clearly distinct ecotypes, residents, transients, and offshores, have

Within the well-studied resident ecotypes inhabiting the Pacific Northwest, animals remain in their natal group for most, if not all, of their life, whereas evidence for the lesser-studied transients and the poorly studied offshores indicates a fluid population structure with temporary or permanent dispersal of offspring from the natal group (Bigg et al. 1987; Ford et al. 1998; Baird 2000; Ford et al. 2000; Dahlheim et al. 2008).

Families or clans are formed from groups of animals that frequently associate along matrilineal lines known as "pods," and groups of geographically cohesive clans form subpopulations (Ford 1991; Riesch et al. 2012). Subpopulations of the same ecotype

reported by Jett and Ventre (2015). Those authors report an overall (captive killer whales worldwide) median age of survival after 1985 of 11.8 years and for all captive-born of 14.1 years. The discrepancy in our findings with that of the aforementioned study is considerable. The initial steep drop in survivorship reported by those authors suggests that they have included all calf births (including calves that died within minutes of birth) in their calculations, a methodology which disallows comparisons of captive and free-ranging survivorship data owing to the lack of observational data for determining survivorship of calves less than 6 months of age (Olesiuk et al. 1990, 2005). If comparisons to free-ranging populations were to be made that include using day 1 at birth for at-risk days, a correction factor for wild population to account for neonatal and early calf loss must be included. When including neonatal loss in the wild population Kaplan–Meier analysis models, we found that at just a 30% incidence of neonatal loss (only ~75% of what has been predicted in the literature—Olesiuk et al. 1990, 2005), the median survivorship of free-ranging populations significantly dropped from 23 to 10 years (SR) and from 29 to 21 years (NR). These estimates are well within the aforementioned range reported for captive killer whales by Jett and Ventre (2015). For SEA captive-born animals, if live birth data include the 2 neonates that died prior to 40 days, the median age for survivorship based on Kaplan–Meier analysis remained at 25 years.

We did not attempt to calculate longevity using life tables as described by Olesiuk et al. (1990, 2005) because, as previously stated, the oldest known-age animals are still living in both the SEA and NSR populations and none have had time to reach age 50. However, if we look at all NSR_i animals, which include animals of estimated age (Olesiuk et al. 1990, 2005), we find that only 3.2% of the total number of animals are greater than 50 years of age. This result is similar to the approximate number of animals reaching greater than age 50 in table 3 from Matkin et al. (2013) and parallels the population structure of known-age NSR and SEA animals where only 2.1% and 3.5%, respectively, of living animals are 40 years and over. Despite only 3.2% of the total NSR_i population being over age 50, three of these animals alive today have been given estimated ages (as of 1 January 2014) of 79 (W03), 86 (L25), and 103 (J02) years (Bigg et al. 1987; Olesiuk et al. 1990). Based on cumulative probability data from Matkin et al. (2013), the odds that these females have reached the aforementioned ages are 1 in 3,052 (W03), 1 in 16,919 (L25), and 1 in 1,382,511 (J02). Given these odds and the population structure, it appears more likely that the estimated ages assigned to these animals at the start of the study period (1973—Bigg et al. 1987; Olesiuk et al. 1990) were inaccurate. Our analysis supports a proposed longevity of between 60 and 70 years for females and 50 and 60 years for males, with the vast majority (> 97%) of animals dying by age 50. This is substantially less than the longevity of 80–90 years for females and 60–70 years for males that have been previously suggested by Olesiuk et al. (1990, 2005). The long-standing question of longevity for the killer whale will be answered definitively only as data from known-age animals continue to be collected.

Reduced male survivability has been well documented in the wild for both killer whales and the bottlenose dolphin (Bigg 1982; Olesiuk et al. 2005; Wells 2009; Matkin et al. 2013; Wells et al. 2013). Based on findings in the present study and those of Wells and Scott (1990) and Wells (2009), sex differences in not only survivability but also population structure and predicted survivorship between these two species are remarkably similar. However, in contrast to these studies, our analyses of captive and free-ranging killer whale populations indicate that significant reductions in male survivability were only detected in the SR population.

The mortality rate index in the SEA population significantly decreased from a high of 4.1 from 1965 to 1979 to a low of 0.6 from 2005 to 2009. Mortality rates of all three 5-year time blocks over the last 15 years for SEA were less than or equal to the expected mortality rates for wild killer whales. The steady decrease in SEA mortality rates over time emphasizes the importance of closely monitoring this statistic, in conjunction with ASR, as a potential indicator of overall population health.

Female sexual maturity as determined by urinary or serum hormone monitoring has previously been reported for founder animals (animals of estimated ages) to occur from 8.3 to 9.0 years of age (Robeck et al. 1993; Katsumata 2010). However, with the maturation of known-age animals in the SEA population ($n = 9$), we were able to accurately establish a minimum (5.7 years) and mean (7.5 years) age at which reproductive maturation can occur. The mean and range of total body length of these animals at sexual maturation was 484 cm and 435–523 cm, respectively. These findings are in agreement with previous postmortem analyses of killer whales from Norwegian waters where animals were observed to be pregnant as early as 15 feet (457.2 cm) in length and based on tooth analysis were estimated to be sexually mature from 6 to 8 years in age (Christensen 1984).

All SEA females ($n = 5$) that were with a proven male at the time of their 1st or 2nd estrus became pregnant. Thus, for wild animals, age at sexual maturity should also approximate age at 1st conception (AFC). However, the AFC for females in the SEA (~10 years) and NSR (~12.1 years) populations were significantly greater than the mean age at sexual maturity for the known-age SEA animals and the AFC reported by Christensen (1984) for adult Norwegian female killer whales. In that population, 50% of all adult Norwegian females were pregnant or lactating between 16 and 17 feet in length or an estimated 8–9 years of age. For SEA animals, this difference in sexual maturation and AFC reflects the fact that just under half of the animals were either not with a breeding male when they first began to cycle or were intentionally separated from a male during estrus (also determined by urinary or serum hormone monitoring). The difference between estimated AFC for NSR killer whales and the observed AFC of Norwegian killer whales may reflect a greater incidence of 1st calf loss for the NSR animals than what has been estimated (i.e., 40%, Olesiuk et al. 1990, 2005) and therefore by underestimating the percentage of 1st calf loss in our formula to estimate the AFC for NSR animals, it is possible that we overestimated the AFC.

However, an alternate hypothesis is that the observed increase in AFC for the NSR population may represent a true delay in sexual maturation as a result of environmental or biological (ecotype) variations, or a combination of the two. Nutritional deficiencies, resulting in decreased postweaning growth rates, are the only consistent environmental-derived factor known to delay the age of puberty across a range of animal species (Kennedy and Mitra 1963; Frisch and McArthur 1974; Ellis and Lawrence 1978; Schillo et al. 1992; Prunier et al. 1993). While reduced food availability has been used as a possible explanation of higher mortality rates in the NSR (Olesiuk et al. 2005; Ford et al. 2009), no evidence was found for prey availability affecting age at maturity in NSR populations (Ward et al. 2009a); however, those authors stated that time intervals may have been insufficient to detect such changes.

The bimodal pattern of fecundity (births) peaking at age 14 and 17 observed for the NSR was similar to that reported by Olesiuk et al. (2005) for the NR population. They attributed the 2nd peak as the point when the youngest animals were having their 2nd calf. We observed the same phenomena with the SEA population. However, the age of the initial peak (~10 years) was earlier than that of the NSR and reflects the differences in age 1st calves were born. In addition, both free-ranging and captive populations in the present study exhibited a significant linear decrease in fecundity until age 40, as has been reported previously for NSR (Olesiuk et al. 2005; Ward et al. 2009a, 2009b) and for the southern Alaska residents (Matkin et al. 2013). This decline in reproductive potential is believed to represent reproductive senescence and is also supported by a significant relationship between increased calving intervals with age in both the SEA and NSR populations evaluated herein. Reproductive senescence in killer whales, often erroneously termed menopause, has been proposed as a relatively unique strategy for the transmission of information related to population fitness (Foster et al. 2012; Brent et al. 2015; Whitehead 2015) or reproductive success (Ward et al. 2009b). However, reproductive and actuarial senescence is common in mammalian species studied to date (for review, see Nussey et al. 2013) and it therefore should not be considered an unexpected finding in killer whales.

Significant differences in AFR based on the mean age at birth of 1st calf were detected between the study populations by using estimated ages (AFR: SEA, 11.1; NSR, 14.5 years) or using the estimation method (AFR_c) as previously described (Olesiuk et al. 2005; Matkin et al. 2013). The SEA AFR_c of 11.0 years was also less than that previously reported for the NSR during a "period of unrestrained growth" (AFR_c: 14.1 ± 0.2 years) or during a "period of stability" (AFR_c: 15.4 ± 0.2 years—Olesiuk et al. 2005). These earlier estimates for the NR and the value we obtained for the NSR (AFR NSR: 14.0 ± 0.02 years) were greater than that which has been observed for the known-age females in the southern Alaska resident population (12.8 ± 0.2 years—Matkin et al. 2013). While the differences in AFR between southern Alaska resident and NSR populations might be attributed to environmental factors, the substantially higher biological potential observed for SEA animals and the North Atlantic killer whales (estimated to occur between 8 and

9 years from Christensen 1984) compared to the NSR animals seem to warrant further investigation. In addition to the nutritional factors previously discussed, environmental contaminants are believed to affect recruitment rates, possibly through increasing the incidence of abortions or early neonatal or calf loss (Ridgway and Reddy 1995; Reijnders 2003), and the NSR are known to have some of the highest concentrations of polychlorinated biphenyls contaminants among marine mammals (Ross et al. 2000). Thus, if the true AFR can be determined for the North Atlantic population, and then compared to the median age at sexual maturity (~8 years—Christensen 1984), it would provide some clues as to the normal rate of fetal and neonatal loss for primiparous cows in the North Atlantic, and consequently help to determine if the gap observed between the AFR of the North Atlantic Type 1 ecotypes (SEA animals) and North Pacific Residents are due to biological variations in maturation rates, or to fetal or neonatal loss in the latter as a result of anthropogenic stressors.

As expected, the MGL of 532 days (range: 473–567 days) in the captive population was similar to previous reports of gestation length from a subset of this population (Duffield et al. 1995; Robeck and Nollens 2013). A mean gestation of 545 days ($n = 4$) was reported for 2 killer whales in another captive population (Katsumata 2010) and falls within the range observed for SEA animals. While no data exist for early neonatal loss in wild killer whales, the 6.5% loss reported herein for SEA is low when compared to a captive population of bottlenose dolphins (2 of 14, 14.3%; under the most current management practices—Venn-Watson et al. 2011a), beluga (3 of 21, 14.3%—Robeck et al. 2005), and to other mammalian species (cattle: 11.7%—Raboisson et al. 2013; horse: 11%—Morley and Townsend 1997; giraffe: 14%—Bercovitch et al. 2004; Asian elephant: 26–29%, African elephant: 12–37%—Saragusty et al. 2009). The CSR to 2 years of age for SEA animals (0.966) was significantly higher than that observed for the SR population (0.799) and but not significantly greater when compared to the NR (0.869). As discussed previously, the differences in neonatal loss and calf survival between captive and free-ranging killer whale populations may be due to a number of factors including nutrition, pollution, or other anthropogenic stressors such as whale watching or other vessel traffic (Ayres et al. 2012).

Our findings provide evidence for the similarity in life-history parameters of known-age animals from captive and free-ranging killer whale populations. These results have application for use in future research concerning the overall health of both populations and provide support for the utility of captive populations as models for understanding the impacts of anthropogenic stressors on free-ranging population physiology and long-term sustainability. Future research with captive populations can be directed toward evaluating methods for detecting early pregnancy and the development of sex-specific fertility potential tests, which if successful, will help population managers further characterize if, when, and how anthropogenic stressors are affecting reproduction in wild killer whales.

