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Whalewatcher

Killer Whale:

The Top, Top Predator

Special Guest Editor
Robert L. Pitman

American Cetacean Society

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Special thanks to Uko Gorter for the cetacean illustrations in this issue, and to the National Oceanic and Atmospheric Administration (NOAA) for its donation towards printing. Cover photo by Bob Pitman.

Photo by Robert Pitman

Dear ACS Member,

I simply could not be more excited or proud to share this issue of *Whalewatcher*, devoted exclusively to killer whales, with you. Intelligent, highly social, magnificently powerful - they are the unchallenged sovereigns of the world's oceans. Killer whales captivate our imaginations - they are our sea-faring counterparts – with stable social bonds, languages, ideas, and behaviors that are passed on from generation to generation. They are, indeed, whales with a culture.

In killer whale societies, as in our own, identity is defined by the company you keep and what you do. It's staggering to imagine how far we've progressed in our understanding of these cognitively complex, ecologically diverse, charismatic creatures. Once universally reviled as voracious, cold-blooded, multifarious predators, we now know that geographically isolated killer whale populations have evolved an incredibly diverse and divergent array of life history strategies, from acoustics, and prey specialization, to behavior and morphological features.

We also now understand that humans and killer whales share much in common – and that some threats to killer whales now intersect with human lives. Persistent, industrial toxins such as PCBs and PBDEs (a group of chemicals used as flame retardants in a wide range of products including clothing, computers, electronic equipment, motor vehicles, carpets, and furniture) have accumulated to such high concentrations in some killer whale populations that individual animals qualify for treatment as "hazardous material." The fate of some populations is determined by the availability of prey species that have been overfished, while still others suffer from habitat degradation.

Our activities are changing the ocean environments in ways that are detrimental and unimaginable, and animals at the top of the marine food chain, like killer whales, quite literally bear the legacy of our past and present mistakes. There may be few other species so like ourselves, and perhaps killer whales and people share another common trait – the ability to connect with and demonstrate empathy toward another species – and each other. In our complicated relationship with nature, it may be a bond unlike any other.

The American Cetacean Society is indebted to Robert Pitman for serving as guest editor of this very special issue, as well as the outstanding array of contributing authors, illustrators, and editorial team. And of course, thank you – for your support of ACS – and for caring about whales, dolphins, porpoises, and the healthy habitats on which they depend.

Executive Director
American Cetacean Society

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An Introduction to the World's Premier Predator

An excited Bigg's ("transient") killer whale eyes the photographer as it searches for a northern fur seal by the side of our research vessel near the Pribilof Islands, Alaska. Photo by R. Pitman, NOAA Alaska Fisheries Science Center, NMFS Permit No. 782-1719

by Robert Pitman

Thirty-five years ago, when I first started going to sea, a quite different killer whale roamed the world's oceans. It was a single, worldwide species and the ultimate omnivore, capable of preying upon any large vertebrate that swam into its purview, including fish, birds, mammals or reptiles. Social behavior revolved around dominant adult males, which used their much larger size and aggressive behavior to take command of harems of females and young - rather like a lion with his pride. Since that time, armadas of dedicated researchers working from small boats have spent countless thousands of hours following killer whales, studying their behavior and learning their ways. Their diligence, aided by burgeoning technologies – satellite tagging, digital photography, and genetic analyses, to name a few – has radically altered our understanding of this animal, and what has emerged is a completely different killer whale – in fact, several.

Killer whales are also called orcas. Many of us who have seen this animal relentlessly battering their prey for hours at a time, sometimes stripping flesh and limbs off live animals, prefer to call them killer whales. Others, perhaps choosing to emphasize the maternalistic social organization of killer whales, and people maybe more familiar with the relatively benign feeding habits of the fish-eating forms, prefer to call them orcas, as in their Latin name – *Orcinus orca*. Historically, these two names have been used interchangeably and the animals that they referred to were generally considered to be just two sides of the same coin. Recent research, however, suggests that these naming preferences and the different perceptions that they represent, may be because these are in fact different coins.

What is an Ecotype?

As detailed in the articles that follow, killer whale communities are often comprised of groups of recognizably different types or forms – forms that, for example, look different and have different prey preferences, feeding habits, and acoustic behaviors. In the northeast Pacific, for example, there are fish-eating "residents," mammal-eating "transients" and the less-commonly encountered "offshores." Although the geographic ranges of these "ecotypes" often overlap at sea, they rarely interact and apparently avoid interbreeding entirely. For most animals, this would be convincing evidence that they are in fact separate species. Killer whales, however, are intelligent, highly social creatures that transmit cultural heritages within family groups that can be stable over decades, and it is possible that they merely choose not to breed with other forms of killer whales. This makes it difficult to determine whether these forms are different species or subspecies, or simply variants within a species. The term "ecotype," then, merely recognizes scientific uncertainty with regard to killer whale diversity, and until we know more about killer whale speciation, the term ecotype will remain a placeholder for a work in progress.

If Looks Could Kill.

Undoubtedly the most striking feature of killer whales is their designer paint job: a boldly contrasting, swirling pattern of black and white seemingly configured to make them as conspicuous in the water as possible. For the supreme hunter of the seas, this seems inexplicably maladaptive - most predators have color patterns that blend in with their surroundings to conceal them from their prey, but killer whale evolution has apparently run off in the opposite direction. This is the kind of counterintuitive observation that sets off alarm bells for biologists: Something interesting is going on here.

Killer whales are cooperative pack hunters – much like wolves – and they need to communicate in order to coordinate their hunting activities, whether they are pursuing prey that is small and fast, or large and powerful (read dangerous). Over longer distances, they resort to vocalizations – their sounds carry for miles underwater even when visibility is reduced to just a few feet. But in the heat of pursuit, at close quarters, in often murky waters, having a conspicuous color pattern with clear landmarks may be an important asset for cooperative prey capture.

For killer whales to conduct a coordinated attack on a prey animal, they need constantly updated information on the orientation, speed and direction of travel of other members of the group, and the color patterning of killer whales seems specifically designed to provide that at a glance. When viewed from the side, the large white flank patch on the tail stock of the killer whale telegraphs changes of speed and direction as the tail oscillates up and down. The tail (or "flukes") itself is black above and white below – an animal behind is also going to immediately detect any changes in speed and direction of an animal in front. When a killer whale turns away sharply, it exposes a flash of white belly; when it angles towards

Bob Pitman is a NOAA Fisheries marine ecologist at the Southwest Fisheries Science Center, La Jolla. When not out studying killer whales, he likes to consort with the prey, such as these Adélie penguins at a colony on the Western Antarctic Peninsula. Photo by Lisa Ballance the viewing animal, it becomes darker as the white belly and sides are obscured. Although these features would also be conspicuous to prey animals, by the time killer whales are close enough for the prey to see them, it is probably already too late for the prey to avoid attack.

In addition to coordinating hunting activities, body coloration in killer whales is probably also useful for social signaling. For example, killer whales often leave tooth rake marks on each other's bodies and appendages. These undoubtedly occur during bouts of play, but sometimes exposed red flesh is visible when the wounds are fresh, a sign of more serious interactions - establishing social order, for example. Not surprisingly, an open mouth is a threat display among dolphins, exposing as it does the aggressor's teeth and perhaps intention. If, as seems likely, killer whales also have an open mouth threat display, then their black upper jaw and a white lower jaw will go a long way to making this signal clear and unambiguous.

Although these thoughts on coloration are mostly speculation, they do suggest that the conspicuous color patterning of killer whales maybe wasn't such a bad idea after all.

Why are Killer Whales Important?

Killer whales are important for several completely different reasons with one of the most obvious being that they are immensely popular with the public. In fact, they have become icons of marine biodiversity – pelagic pandas. With their enormous size and stunning black and white color patterning, they are probably the most universally recognizable animals that live in the sea, or perhaps anywhere on the planet. Add to that, they are predators nonpareil – the largest top carnivores on the earth today, with killing power that probably hasn't been rivaled since dinosaurs quit the earth 65 million years ago. Although these out-sized physical attributes make killer whales arguably the most spectacular animals anywhere in the world today, it is perhaps their more subtle traits that make them so compelling: they are intelligent, long-lived, cooperatively-hunting, intensely social animals – they are enough like humans that we are fascinated by them. People want to know more about them and they also want to know that they aren't being harmed.

Killer whales are also exemplars of how little we know about the ocean environment that largely envelops our planet. Not only are they the most widespread large animals on the planet, but as air-breathers they are conspicuous and eminently identifiable. Consequently, they have been studied by numerous people around the globe, for decades in some cases. And yet scientists cannot say with any certainty even how many species of killer whales there are – there could be one, or five, or maybe more. And, if so little is known about perhaps the most charismatic, widespread, easily recognized and well-studied species of animal that lives in the seas, then what do we really know about those millions of other, less-heralded species?

The question of how many species of animals we can identify in the ocean clearly has important conservation implications. If, for example, there is only one species of killer whale and it ranges around the world and has a varied and changeable diet, then local extinctions due to the combined effects of, say, fishery impacts (e.g, through bycatch or prey reduction), marine pollution, climate change, ship collisions, etc., are probably not going to critically impact this species. But, if

A BBC film crew with an underwater "polecam" is dwarfed by a passing adult male type B killer whale in Antarctica. The series producer has covered her head to watch on the monitor. Photo by Bob Pitman there are multiple species, with smaller population sizes, more limited ranges and specialized feeding habits, then localized extinctions could result in the elimination of entire species. Such "cryptic" species can blink out without us even knowing they ever existed.

Killer whales are also important because of their role in marine ecosystems. As large, warm-blooded, apex predators, they necessarily have voracious appetites, making them potentially important in regulating their prey populations, including commercial fish species (e.g., salmon, bluefin tuna) and protected – and sometimes endangered – marine mammal populations (seals, sea lions, sea otters, whales, etc.). The potential for conflict with human interests is, of course, high and the more we know about ecology, taxonomy, distribution and abundance of killer whales, the more we can do to head off these conflicts.

To Have and to Hold

Not all killer whales live in the ocean and keeping them in captivity has always been a contentious issue. The first (and too often, only) exposure many people get to killer whales are with captives serving life sentences in aquaria, for crimes they did not commit. For an animal that can travel 200 or more miles a day in the wild and that would normally spend 50 years or more in a stable family group, hunting cooperatively and engaging in complex social interactions with others of its own kind, a solitary life cooped up in a chlorinated cubbyhole, performing the same tricks day after day for a bucket of dead fish, must be a life unfulfilled. On the other hand, for the majority of the land-locked public, a captive killer whale may be the only opportunity many of them will ever have to experience this magnificent animal. And just as we willingly cut down trees to produce books (and this issue of *Whalewatcher*), a few killer whales sacrificed to educate, perhaps enlighten (and, yes, entertain) the public, may serve to inspire the next generation of marine mammal advocates. It is a necessary evil that we should all grudgingly embrace.

The Known and the Unknown

As is often the case in research, we find that the more we know about killer whales, the less we know about them; every answer asks more questions. In the following pages, we summarize the history of modern killer whale research, describe some of the most significant findings unearthed along the way, and provide recent updates on what it is we know and don't know about these fascinating animals. Most of what we have learned about killer whales has come to light only in the last 20-30 years, and many of the people behind that research are still active in the field today. We are fortunate that several of them have offered to share their insights and experiences in these pages.

A calf Ross Sea killer whale (Antarctic type C) takes a long look at whale researcher, and Bob's wife, Lisa Ballance, in a fast ice lead in McMurdo Sound. Photo by Bob Pitman

We are also very fortunate that Uko Gorter has once again offered up his time and artistic talent to illustrate this special issue. The centerfold he has produced represents not only an up-to-date sampler of killer whale diversity as currently understood, but it shows the various types, for the first time, drawn to scale.

I think I speak on behalf of all the contributors to this issue when I say that killer whales are the most amazing animals that currently live on this planet, and if you haven't already, you owe it to yourself to see this animal in the wild. You won't be disappointed.

ACS sends very special thanks to Bob Pitman and all of the contributing authors for this one-of-a-kind Whalewatcher issue. Photo by Bob Pitman

How Do We Study Killer Whales?

by John Durban and Volker Deecke

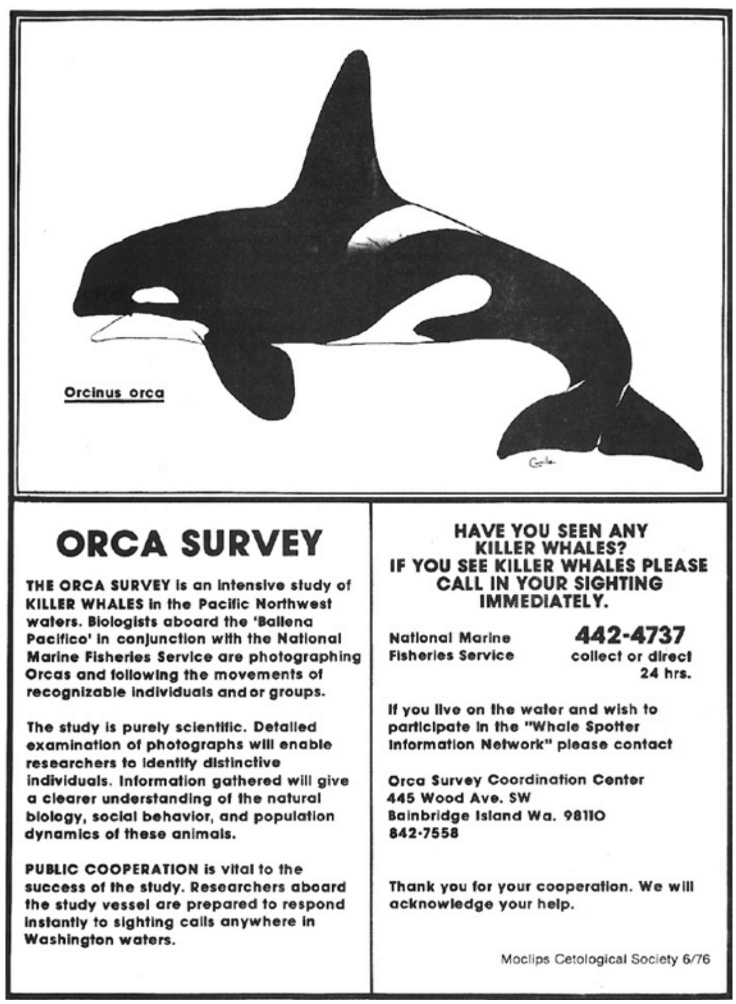
Killer whales are the top predators in the world's oceans, abundant in some areas, and perhaps the most recognizable animal on the planet. It may therefore seem somewhat of a surprise that they are difficult to study. However, they are capable of rapid and long range movements, can be cryptic and hard to observe when they hunt and feed underwater, and are found at highest density in productive high-latitude areas, which can be hard to work in due to their remoteness and challenging weather conditions. Nonetheless, this challenge has inspired two generations of field biologists and naturalists to devote their lives and energy to learning about these most impressive of mammals. To do so, we have developed some innovative and state-of-the art research approaches, which we will describe here.

Citizen Science

Research on killer whales is not the sole purview of professional scientists. In more accessible areas, the public has long contributed to our understanding of killer whales by reporting sightings and collecting photographs. In the early 1970s, Mike Bigg and colleagues working with the Canadian Department of Fisheries and Oceans (DFO), and their US counterpart, Ken Balcomb, then working under contract from the National Marine Fisheries Service (NMFS), established public sighting networks as a first step in long-term studies of killer whales in the northeastern Pacific. Sighting networks continue to provide the basis for monitoring studies, even in remote areas like Antarctica, where cruise ship passengers regularly collect sightings and photographs.

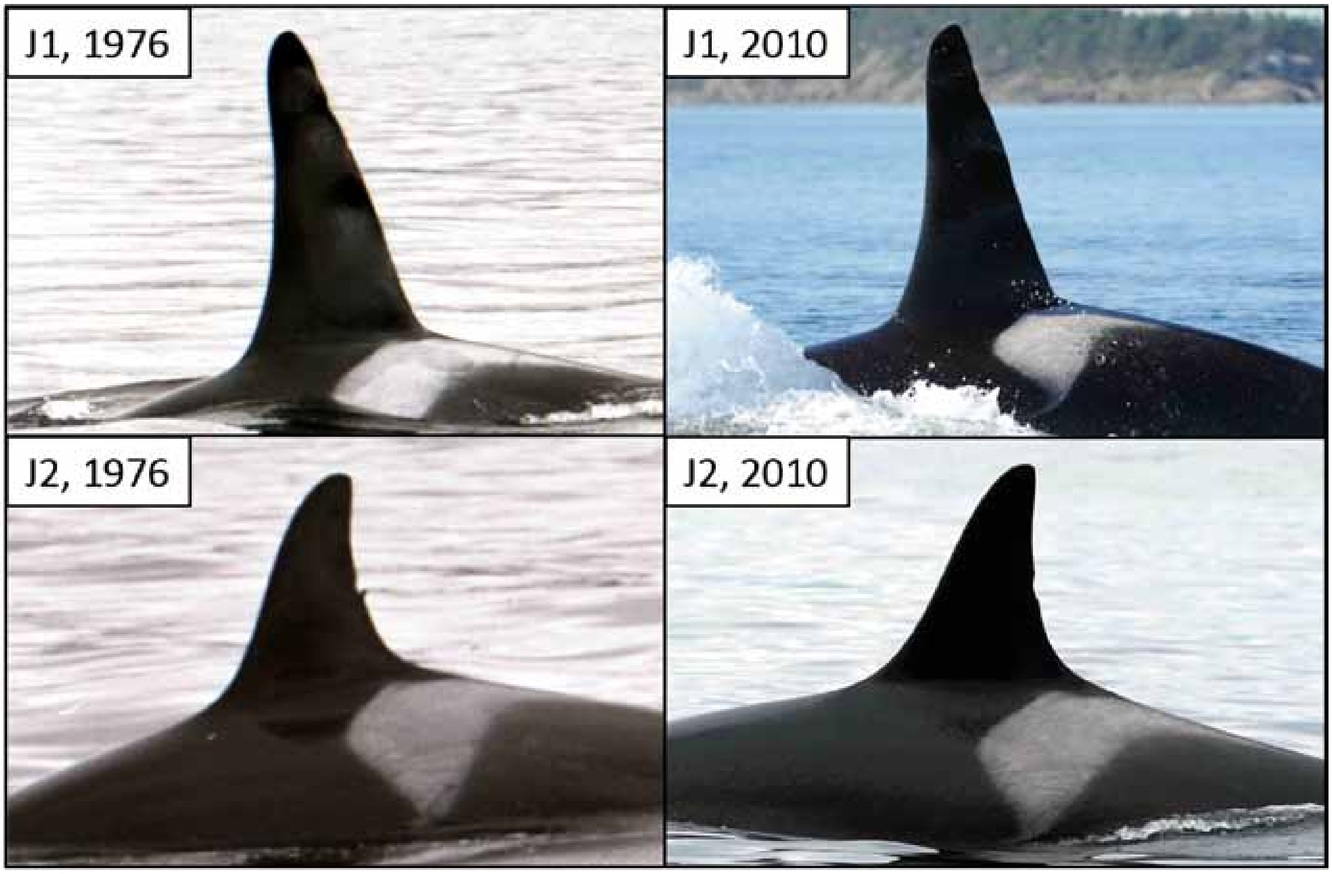
Photo-identification

Although sighting data have been useful for identifying areas of regular use by killer whales, population studies have benefitted most from the discovery that individual whales could be readily distinguished from natural markings; specifically, variability in the shape of the dorsal fin, pigmentation of the adjacent saddle patch, and naturally acquired nicks in the dorsal fin. Mike Bigg developed the tool of photo-identification in the early 1970s using these features to identify individual killer whales from photographs. At the same time, this approach was being developed in studies of humpback whales, right whales and bottlenose dolphins off the east coast of the US. These are not the earliest examples of using natural markings to document individual killer whales: hand-drawn illustrations by Clifford Carl documented individual variability in eye patch pigmentation within a group of killer whales stranded at Estevan Point on Vancouver Island in the 1940s. Ken Balcomb



Have you seen me? Poster distributed in the Pacific Northwest in 1976 requesting information from the public about killer whale sightings. Courtesy of Ken Balcomb, Center for Whale Research, WA.

and colleagues at the Center for Whale Research (CWR), WA., have now used eye patch distinctiveness to document the individual identify of killer whales netted during live-capture fisheries in British Columbia and Washington State in the early 1970s, by comparing archival images to a catalog of eye patch photographs from extant whales. Eyepatches are still the best way to identify very young killer whales before the saddle patch pigmentation develops and the animals acquire characteristic scars.



Fin and saddle patch photo-identification images, with long-term photographic re-sightings of an adult male "southern resident" killer whale (J1, top) and an adult female (J2, bottom) in 1976 (left) and again in 2010 (right), demonstrating the longevity of these distinctive natural markings. Courtesy of Ken Balcomb, Center for Whale Research, WA.

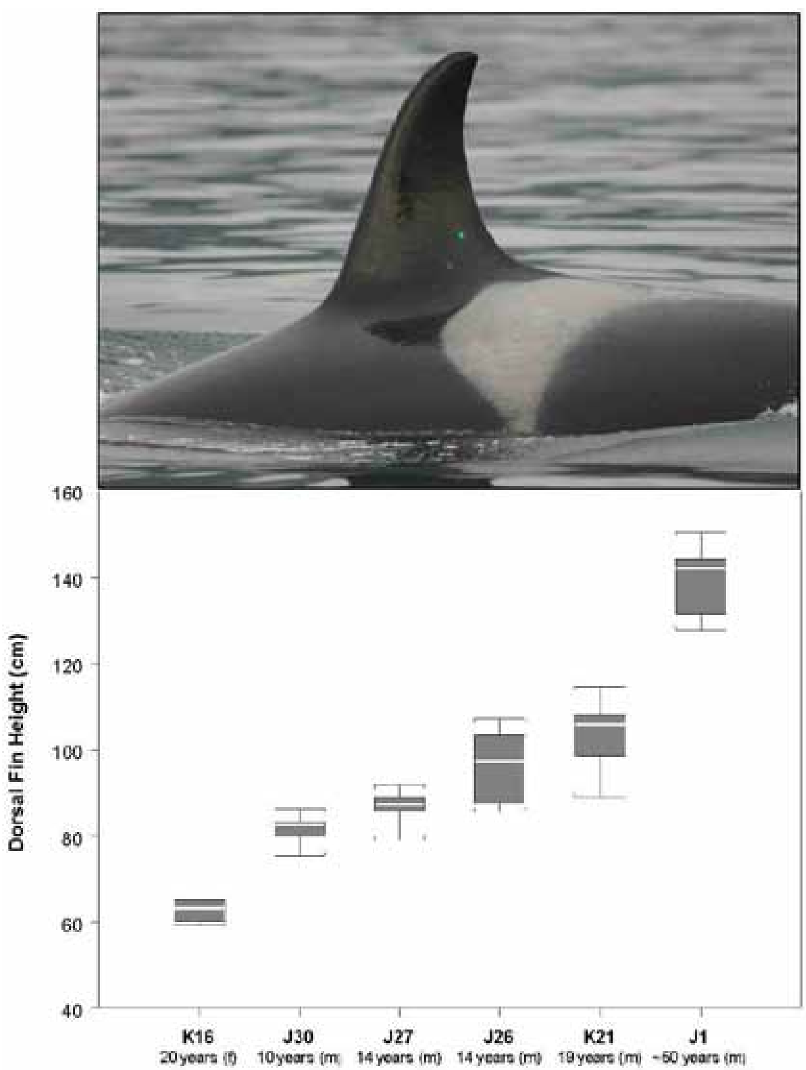
Photo-identification has become the stock tool for research on killer whales, with individual recognition underpinning the majority of studies we conduct around the world. Using long-term photographic records of the same individuals (dating back as far as the late 1950s for "transient" killer whales in the northeastern Pacific), has proven this to be a robust method for individual-based monitoring over the long time periods required to study killer whales with life spans similar to humans. Thanks to diligent and skilled photo analysts like Graeme Ellis (DFO) and Dave Ellifrit (CWR), we now have long-term photo-id datasets that can be used to understand life histories and population dynamics, long-term changes in social structure, and movement patterns. In more remote regions, where it hasn't been possible to conduct full photographic population censuses, John Durban (NMFS) and colleagues have shown how repeated photo-identifications of the same whales have been used as "captures" and "recaptures" in mark-recapture models for estimating abundance and movements.

The ability to recognize individual whales at sea has captivated researchers and the public alike, providing a connection to the individuality of the whales. In his seminal 1987 book, *"Killer whales: A study of their identification, genealogy, and natural history in British Columbia and Washington State,"* Mike Bigg described the excitement during the early moments of a killer whale encounter when the individual identity of the whales was revealed. The advent of digital cameras and access to established photo-identification catalogs now provides this instant reward to a growing third generation of killer whale addicts, continuing to foster a sense of familiarity, interest and "ownership" in killer whale populations worldwide. This level of interest is of great help to researchers, as there are increasing numbers of public naturalists collecting identification photographs which can be used in scientific studies.

In addition to the identification of individual whales from photographs, images can also be useful for identifying killer whales to "type." For example, experienced observers in the northeastern Pacific can differentiate whales from "resident," "transient" and "offshore" killer whale lineages by appearance, and Bob Pitman and colleagues have used a collection of photographs from Antarctic and Southern Ocean waters to describe at least four different types of killer whales based on morphological differences, providing an early clue to genetic differentiation.

Photogrammetry

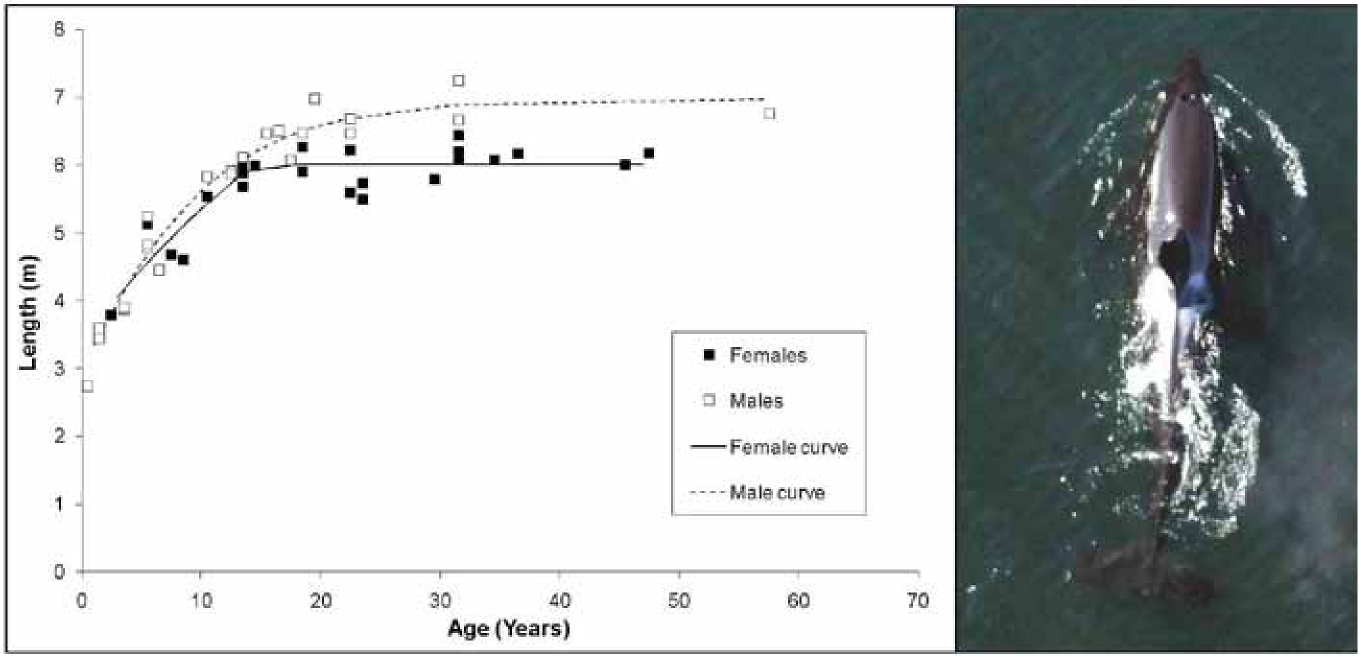
As top predators, there is considerable research interest in the prey requirements of killer whales, so that we can evaluate their predation impact on endangered marine species and detect threats to killer whales from prey shortages. This requires information on the size, growth and body condition of killer whales. John Durban and Kim Parsons, working with NMFS and CWR, developed a novel approach for obtaining morphometric measurements using two parallel laser-beam pointers to project a scale of known size that can be photographed on the whale's fin or body, and this is now being used to obtain measurements from several killer whale populations around the world. The advantage to this approach is that it can be implemented alongside photo-identification studies to monitor the long-term growth of identified individuals.



Two green laser-dots of 10cm separation projected onto the fin of an adult female killer whale to provide a scale of known size (top); repeated measurements of dorsal fin height using laser-metrics for 6 southern resident killer whales of varying age and sex (bottom). Adapted from Durban and Parsons, 2006. Marine Mammal Science 22:735-743 (Photo by John Durban, Center for Whale Research, WA).

However, it has not been possible to measure total body length using the laser-metric approach because parts of the whale remain submerged, although length can be estimated if body proportions are known. Similarly, width measurements are unavailable, and these may be particularly useful for assessing changes in body condition. However, both these measurements can be directly estimated using aerial photogrammetry, where an aircraft is used to obtain high-quality images from directly above whales, and the altitude of the aircraft and focal length of the lens can be used to scale the image to a real size. Bob Pitman and colleagues first used this approach to measure body lengths of killer whales in Antarctica, and recently Holly Fearnbach, John Durban and CWR colleagues matched aerial photogrammetry images to a saddle-patch identification catalogue to obtain length and width measurements from known southern resident killer whales in WA and BC waters, so that size-at-age could be estimated to evaluate long-term growth trends.

Knowledge of the size and body proportions of killer whales around the world can also help to refine our understanding of the taxonomic divisions within killer whales – together with genetic differences this information can be used to suggest different lineages, which may represent different species. Bob Pitman's aerial photogrammetry study showed that

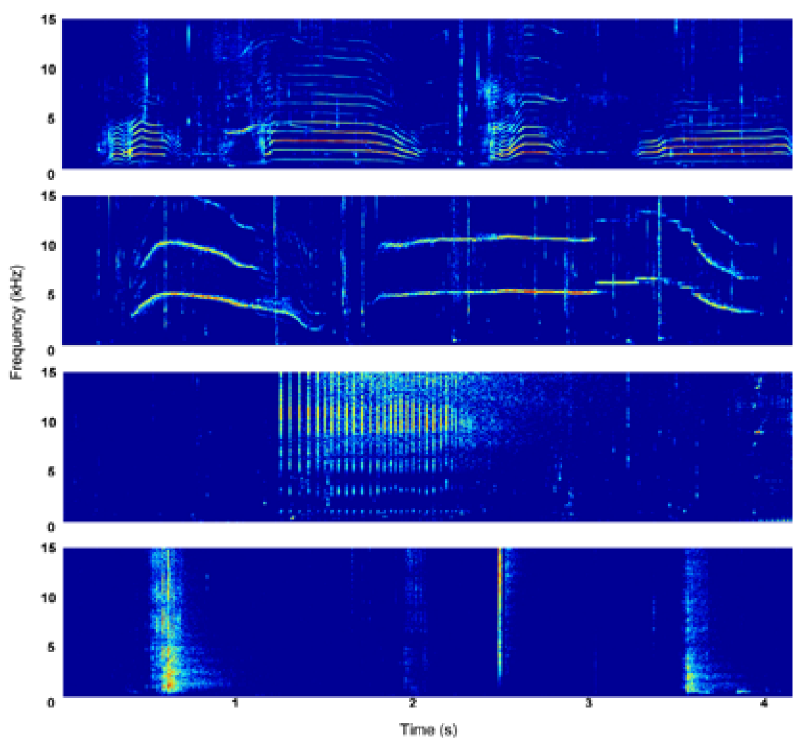


Total body length for southern resident killer whales of known age (left), estimated from aerial photogrammetric images of individually-identifiable whales taken from a helicopter at known altitude (right). Adapted from Fearnbach et al. 2011. Endangered Species Research 13: 173-180 (Photo by Holly Fearnbach, Center for Whale Research, WA).

Antarctic type C killer whales from the Ross Sea are significantly smaller than killer whales measured elsewhere, further supporting genetic inference that "Ross Sea Killer whales" may be a distinct species. Aerial measurements, laser measurements and the size of stranded animals have been used to scale Uko Gorter's fantastic illustrations of the world's (currently recognized) killer whale ecotypes, which form the centerfold of this special issue.

Acoustic Research on Killer Whales

Much like we can identify individual killer whales from natural markings and can tell different populations and lineages of killer whales apart from the way they look, we can use sound to identify killer whale groups. Like other dolphins, killer whales produce three types of sounds. *Echolocation clicks* primarily function in orientation and prey detection: the animals emit these sounds and listen to the echoes reflect from objects which they use to obtain a three dimensional representation of their surroundings. *Whistles* are high frequency sounds that are probably used in communication over relatively short distances whereas *pulsed calls* are long-range communication signals that killer whales use to communicate over



Spectrograms of (from the top down): pulsed calls, whistles, echolocation clicks and prey-handling sounds recorded from transient killer whales.

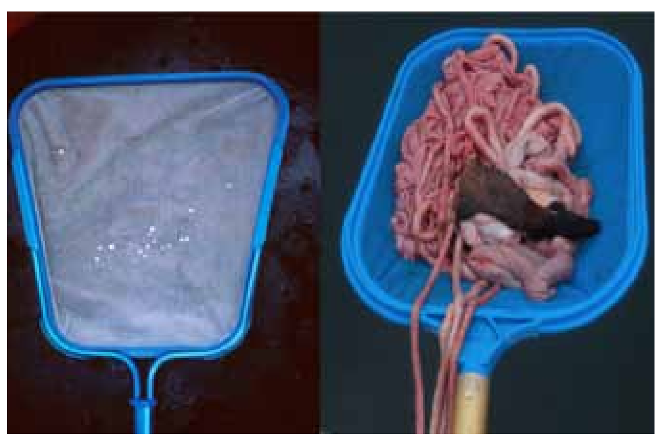
tens of miles. John Ford and Dean Fisher at the University of British Columbia first showed that killer whales have group-specific repertoires of stereotyped pulsed calls that we can use to tell different populations apart. Ford found that in some populations these dialects are so variable that we can use them to identify individual family groups. This means that we can track the movements of such groups with a minimum of field work, simply by deploying autonomous recording devices in strategic locations throughout their range. These devices are mounted on the sea floor, make a short recording at set intervals and can be deployed for up to a year. Once the devices are recovered and the data downloaded, the stereotyped call types in the recordings can tell us when certain killer whale groups passed in the vicinity of the recording device.

Observations of Predation and Prey Sample Collection

Knowledge of the predatory role of killer whales clearly requires data on diet and prey preferences. The most direct source of data are observations of hunting and feeding behavior, which are easiest to make when killer whales capture big prey, such as large whales, or seals that can be observed to be taken from ice floes. However, even then these observations can be scarce and hunting/feeding behavior can be cryptic and hard to interpret. Observing kills requires long hours of effort, and careful observation protocols – for example, being far enough away to not disrupt hunting but close enough to confirm the prey species taken. Confirming kills requires robust standards for observational data, for example seeing the prey being broken up or consumed, generally involving the presence of birds and an oil sheen on the surface of the water, which is often associated with a fishy odor. Without these signs, it cannot be clear if a successful predation event occurred, or if the prey escaped. Such clear observations of predation can be rare to acquire – for example, it took more than ten years of observations before transient killer whales in the northeastern Pacific were confirmed to take marine mammal prey.

Rather than looking for signs of killer whale kills, a better strategy may be to listen for them. Work by Lance Barrett-Lennard and Volker Deecke has shown that killer whales hunting marine mammals typically keep quiet when searching for prey but produce calls, whistles and echolocation clicks after a successful kill. While many fishes have poor hearing abilities, all marine mammals have excellent underwater hearing and can probably detect killer whale sounds over significant distances. This means that mammal-eating killer whales need to rely on stealth to get close to their prey, but start calling, whistling and clicking once an attack has been successful. Researchers can follow groups of killer whales while monitoring their vocal behavior with hydrophones and use such bouts of vocalizations as an indicator that a kill has occurred. Using this approach, Volker Deecke and colleagues have shown that groups of killer whales dismembering a marine mammal carcass also generate characteristic cracking and crunching sounds as bones are broken and blubber is stripped and these so-called Killing, Ramming and Crushing Sounds (KRaCS) are a clear indicator that an attack was successful. We can even use sound to study killer whale diets by asking potential prey species how they feel about certain killer whale groups: harbor seals in the Northeast Pacific for example respond very strongly to the calls of mammal-eating transient killer whales, but completely ignore the harmless fish-eating residents.

Once a kill has been confirmed through observation or listening, it has become standard to collect prey fragments, which can be used to identify the prey species. For example, John Ford, Graeme Ellis and colleagues have collected fish scales and tissue fragments from the vicinity of feeding eastern North Pacific resident killer whales for almost 40 years: scale analysis and aging techniques have been used to assess both the species and age of fish taken. Molecular genetic analysis has further been used to confirm species identity from both scales and tissue and in the case of Pacific salmon, can even tell which river the salmon spawn in. Marine mammal prey have also been identified using molecular genetic analyses of prey remains, notably in a study of transient killer whales feeding on submerged carcasses around Unimak Island, Alaska, where Lance Barrett-Lennard and colleagues used molecular genetic analyses of surfacing chunks of tissue to confirm that the carcasses belonged to gray whales. A similar method was used to confirm sharks, particularly sleeper sharks, as a key



Prey remains recovered from killer whale kills for genetic analysis to determine the prey species: Chinook salmon scales on the left; Steller sea lion remains on the right (Photo courtesy Lance Barrett-Lennard and Volker Deecke).

prey item of offshore killer whales in the northeastern Pacific, allowing quantification of the number of individuals taken during an eight-hour encounter.

Recently, the collection and analysis of killer whale feces has been developed as a further source of direct data on killer whale prey habits. NMFS scientist Brad Hanson and colleagues working in the San Juan Islands, WA, have demonstrated how fecal samples can be collected by patiently following behind the whales, with co-workers from Sam Wasser's laboratory at the University of Washington using a trained sniffer dog (a black Labrador retriever) to increase the number of samples collected.

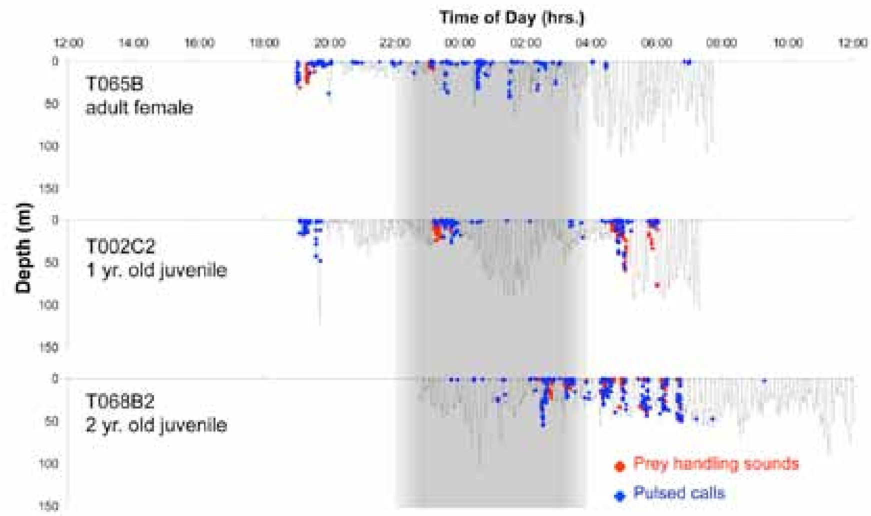
Juvenile killer whale equipped with a digital recording tag. The tag is attached by four suction cups and records the whale's underwater movements as well as any sounds it makes or hears. Photo by Volker Deecke

Molecular genetic techniques can then be used to amplify the DNA of partially-digested prey species, as well as killer whale DNA from sloughed cells of the gut lining. The same fecal samples are currently being used to measure stress hormone levels of whales relative to periods of food limitation, and to conduct hormone assays to assess reproductive status.

Suction Cup and D-tags

A persistent problem when studying the behavior of killer whales and other cetaceans is that most of it happens underwater and out of our view. Listening to whales rather than looking at them is one approach to address this challenge, however, recent technological advances offer even more exciting insights into the underwater behavior of killer whales. Miniaturization of sensors and electronic components has led to the development of data loggers small enough that they can be attached to killer whales non-invasively with suction cups. Robin Baird, working with Simon Fraser University in Burnaby and Dalhousie University in Halifax, was the first to attach time-depth recorders to killer whales to investigate their diving behavior. That study documented significant differences in the diving behavior of males and females.

A sophisticated D-tag developed by Mark Johnson and Peter Tyack at Woods Hole Oceanographic Institution not only records continuous time and depth, but also carries a compass and acceleration sensors to record the three-dimensional movements of tagged killer whales at very high resolutions (enough to resolve individual fluke beats). In addition, the tag has two built-in hydrophones and can record high-quality underwater sound for up to 24 hours allowing us to detect any sound the tagged individual produces or hears. For the very first time this tag therefore enables us to correlate vocal behavior and underwater movements of killer whales providing exciting insights into how these animals use sound to coordinate movements and how they respond to sound stimuli in their environment. Volker Deecke, Patrick Miller and colleagues have used such digital



Dive profiles of three transient killer whales outfitted with digital recording tags in Southeast Alaska. Gray shading indicates the hours of darkness. Red diamonds designate characteristic crunching sounds indicative of a marine mammal kill, blue diamonds designate bouts of vocal behavior. Courtesy of Volker Deecke

recording tags to study the night-time behavior of transient killer whales in Southeast Alaska. The tags allowed them to document successful attacks even in complete darkness by listening for bouts of vocal behavior and characteristic crunching sounds generated during prey handling. This showed that transients are also able to find and capture marine mammals at night without needing vision to locate their prey.

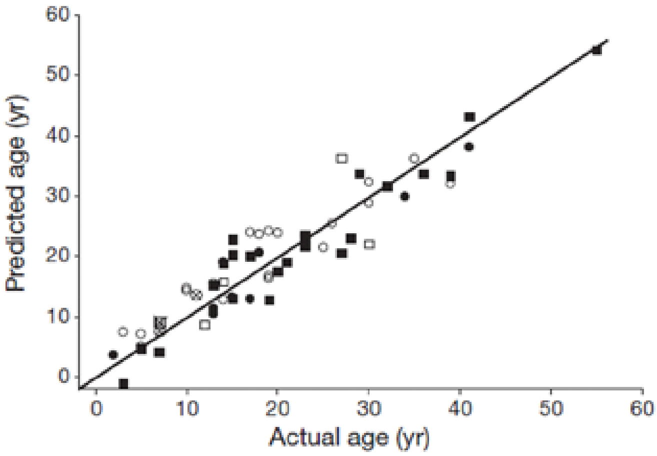
Biopsy Sampling

In the 1990s, Lance Barrett-Lennard from the University of British Columbia and colleagues at DFO developed a remote biopsy system using a lightweight dart to collect a skin and blubber sample from free-swimming killer whales. At the time, no one could have imagined the range of studies that would be possible using this small tissue sample, about the size of a pencil eraser. Now, hundreds of biopsy samples have been collected from killer whales throughout the world, enabling a whole suite of laboratory-based analyses to assess dietary preferences, contaminant loads, approximate age, patterns of relatedness, population structure and species identity.

Dietary preferences can be inferred through chemical analyses of fatty acid composition of the blubber portion of the biopsy sample, as well as stable isotope ratios in the skin plug. Notably this has been used by Peggy Krahn, David Herman (NMFS) and colleagues, who were able to use these chemical signals to document the persistent prey specializations of residents (fish) and transients (marine mammals) over a wide area of the North Pacific, and to infer that the diet of transients was comprised of a variety of marine mammal prey, not solely or primarily endangered Steller sea lions. These qualitative inferences are a useful supplement to direct observations of predation and prey sample collection, which have been limited in remote waters.

A surprising, but powerful, discovery was that it is possible to estimate the age of killer whales from their blubber fatty acid compositions. This discovery was made by David Herman and colleagues during investigations of diet, and was validated by examining the estimates for animals of known age from long-term photo-identification studies. Relatively precise estimates (within three years of the known age) were possible for males and females of both residents and transients, demonstrating the general utility of this approach. This technique therefore allows aging and age structure analysis

A small 9g biopsy dart (orange tail) is fired by a pneumatic rifle and bounces off the saddle of a transient killer whale in Alaska, with a small inch-long cutting tip collecting a 0.5g plug of skin and blubber for a suite of laboratory analyses. Photo by Dave Ellifrit, NOAA Alaska Fisheries Science Center, NMFS Permit No. 782-1719



Plot showing the significant relationship between the actual ages of 59 known-age resident and transient killer whales and the ages predicted from their outer blubber fatty acid compositions. Adapted from Herman et al. 2008, Marine Ecology Progress Series 372:289-302

in populations for which long-term demographic monitoring has not been possible, and has been used to compare the age composition of transient and resident populations in the Gulf of Alaska and Aleutian Islands.

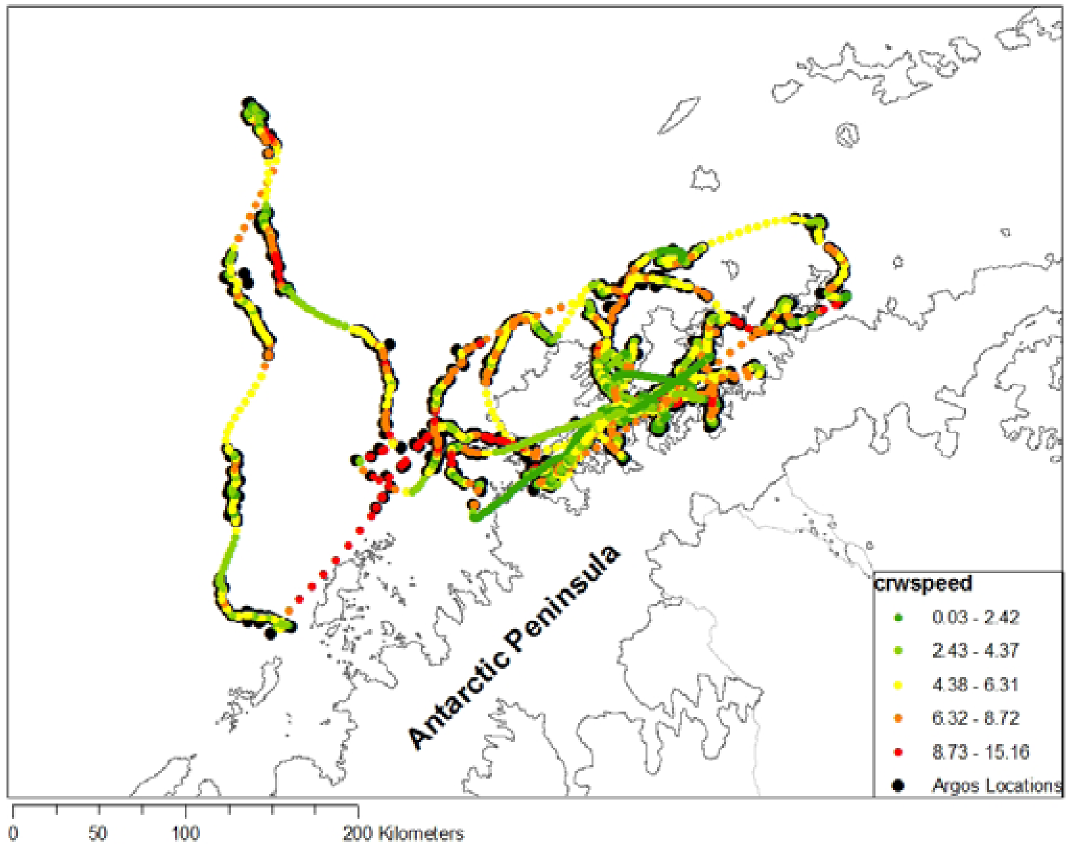
Persistent organic pollutants (POPs) are acquired when killer whales eat contaminated prey, and accumulate in their blubber layers throughout their lives. Peter Ross and colleagues at DFO first measured high concentrations of POPs (e.g. PCBs) in blubber biopsy samples of killer whales, highlighting potential health risks if and when these blubber fat stores are metabolized and when fat is passed from lactating females to their young. Peggy Krahn, Gina Ylitalo and colleagues at NMFS have also shown how POP "signatures" can be traced to pollution sources and therefore used to infer feeding in specific regions. For example, they have identified a "California signature" to infer repeated feeding in California Current waters by part of the endangered southern resident killer whale population that is more regularly encountered off Washington and British Colombia during the summer months.

Molecular genetic analysis of killer whale DNA was the first use of skin biopsies, but is also an approach that continues to develop and provide fascinating insights. Lance Barrett-Lennard used genetics to assess patterns of relatedness within and between killer whale populations in the northeastern Pacific, including examining the mating systems of killer whales by identifying parentage. This work on population structure is now being extended by Kim Parsons and colleagues working more widely in the North Pacific, and is also being conducted in the North Atlantic by Andy Foote and co-workers. Genetics can also be used to infer the evolutionary relationships of different killer whale populations, and recent sequencing of the full mitochondrial genome has provided sufficient detail to perform an examination of worldwide relationships among killer whales, suggesting the possible existence of multiple species. Intriguingly, the same sequences can be used to examine parts of the genome that are under selection – for example, Andy Foote and colleagues have recently shown that the two types of killer whales regularly encountered in icy Antarctic waters (types B and C) are under selection for altered cellular metabolism, perhaps an adaptation to living in the extreme cold. We expect further investigation will provide some key insights into the evolution of killer whales, offering clues to their success in occupying the varied habitats of all the world's oceans.

Satellite Telemetry

Understanding the ecological impact of killer whale predation, the factors determining their distribution and the relationship between killer whale types requires data on their movements. Although it is possible to infer the movements of some populations from intensive and long-term photo-identification efforts, this is generally not the case, particularly in remote environments, challenging winter seasons, or new study areas. In these situations, satellite transmitter tags have emerged as a practical tool for directly monitoring movements beyond the time frames possible in costly field surveys. Recent advances in satellite tag electronics have allowed tags to be developed that are small enough to be deployed externally on the dorsal fin using crossbows or pneumatic rifles, without the need for physical capture and restraint. Specifically, Russ Andrews from the Alaska SeaLife Center and University of Alaska

A small 40g satellite LIMPET tag attached to the dorsal fin of an adult male transient killer whale in Alaska. The red arrow indicates the tag location. Photo by John Durban, NOAA Alaska Fisheries Science Center, NMFS Permit No.782-1719



Movement track of a type A killer whale on the western side of the Antarctic Peninsula over a 44-day deployment of a satellite LIMPET tag. Closed black circles show locations calculated by satellite receptions of tag transmissions, and a movement model has been used to estimate displacement speeds (in km/hr) along the track. Courtesy of John Durban, NOAA Southwest Fisheries Science Center.

in Fairbanks has developed a Low Impact Minimally Percutaneous External Transmitter (LIMPET) tag, which attaches to the outside of the dorsal fin using two titanium barbs. More than 50 of these small, 40g tags (smaller than a standard box of matches) have now been deployed on killer whales, primarily in remote study areas in Alaska and Antarctica, with tag longevity of more than 100 days and tracked individual movements of more than 9000 km (5,600 miles).

Regular transmissions from these tags can be used to provide information on fine-scale movements and habitat use. Furthermore, these transmissions can be received by satellites and processed in near real-time, which can be used to guide field teams to find whales for more frequent observations. For example, Bob Pitman and John Durban were able to use satellite tag locations to re-find focal groups of type B killer whales in the Antarctic pack-ice almost daily over multiple weeks to greatly increase the number of feeding observations possible in this challenging environment. With continued advances in electronic miniaturization and battery technologies, we expect future versions of LIMPET tags to be even smaller, and also to incorporate additional sensors to study diving behavior and relatively fine-scale changes in movement, further providing a window for remotely viewing the behavior of killer whales.

An Ongoing Legacy

We are indebted to the pioneers of killer whale research – Mike Bigg, Graeme Ellis, Ken Balcomb and John Ford. We have learned from them, been inspired by their work and commitment, and we try to follow their example. We now have a growing toolbox of research methods which we can use to unveil the fascinating lives of killer whales around the world. We hope this special edition will similarly inspire a new generation of killer whale researchers to join in this challenge.

Killer Whales of the Pacific Northwest Coast:

From Pest to Paragon

A portrait of a (northern) resident pod off the west coast of Vancouver Island. Photo by Brian Gisborne

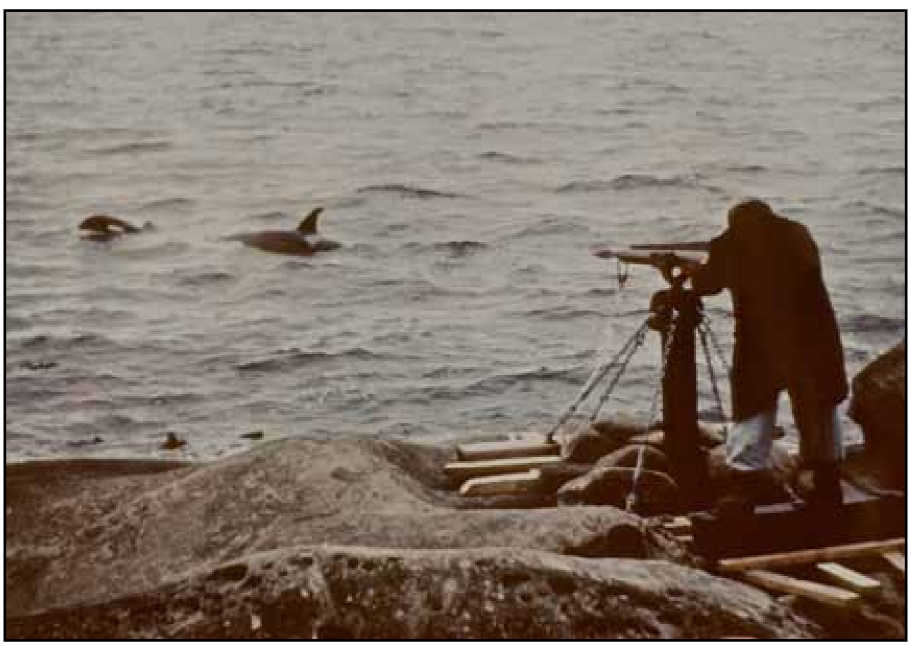
by John K.B. Ford

The nearshore waters off the Pacific Northwest coast are known internationally as one of the best places – if not THE best place – to view killer whales in the wild. Each summer, legions of whale watchers head out in tour boats, private boats, and sea kayaks to the protected waters around the San Juan Islands of Washington State or Johnstone Strait in British Columbia, in the hope of experiencing these dramatic predators in their natural habitat. Thousands of killer whale enthusiasts follow the daily movements of local pods on orcanetwork.org, an on-line repository for sighting reports, or listen to the whales' underwater conversations from hydrophone signals streamed live on the orca-live.net or orcasound.net websites. Killer whales have become more than just high-profile icons of the wild Pacific Northwest – some of the better known individuals have attained celebrity status among orca aficionados. These days, even the death of an old matriarch or bull in the well-known "southern residents" is front-page news in local media.

Given the current fame surrounding killer whales of the Northwest Coast, it is remarkable that just a few decades ago – well within the lifetime of the older whales in the population – these animals were widely feared and despised. Many people considered them to be serious threats to safety that would, if given the chance, attack humans in the water without hesitation.

A popular book on dangerous sea creatures written in the 1960s claimed that the orca was the "biggest confirmed man eater in the oceans." Although in fact there were no substantiated cases of this happening, with the name "killer," who was to question this fearsome reputation? Many people along the coast also held killer whales in contempt as unfair competitors for salmon and they were commonly shot by fishermen, as were other predators such as seals and sea lions. Even the Canadian Department of Fisheries was intent on persecuting killer whales. In 1961, the agency installed a 0.50-calibre machine gun on shore at Seymour Narrows, a constriction in the inside passage off the east side of Vancouver Island, in order to kill or drive killer whales away from the Campbell River area (an earlier idea to launch mortars at them lost out to the machine gun approach). Evidently, the whales had spent the previous few summers harassing and frightening guests at salmon fishing lodges by taking fish from their lines. Although the gun was used for some target practice, the whales didn't show up that year and the culling program was abandoned.

The negative attitude toward killer whales that prevailed in the early 1960s was mostly due to their reputed ferocity and prodigious appetite, both of which had grown to mythical proportions from the highly embellished tales of mariners over the centuries. Scientifically, virtually nothing was known about the species' life history, ecology and behavior. Given this attitude, there was little objection when the Vancouver Aquarium made plans to collect a killer whale specimen by harpoon in order to create a biologically accurate, life-sized display model of the species. In the summer of 1964, the collectors set up a harpoon gun on the shore of Saturna Island in the Canadian Gulf Islands, and waited for a killer whale to come within range. Several weeks later, a young whale did so and it was harpooned, wounding but not killing the animal. Upon realizing that they now had a live killer whale on their hands, a quick change of plans was made and efforts shifted to keeping it alive for public display. The injured whale was led by the harpoon line to Vancouver harbour where "Moby Doll," who was thought to be female, was housed in a floating net pen. He (it turned out to be a young male) lived there for several months before succumbing to an infection.



The harpooning of "Moby Doll," the first killer whale to be displayed in captivity, Saturna Island July 1964. Photo by J. Bauer

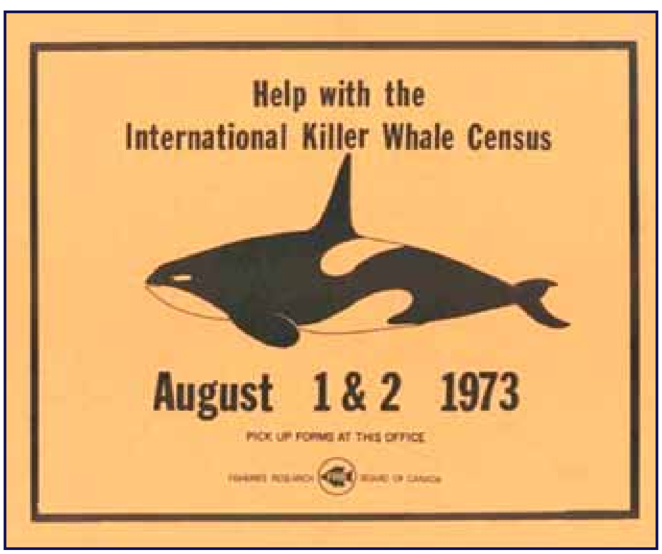
The capture of Moby Doll was pivotal in our relationship with the killer whale. This was the first time a live killer whale could be observed at close hand by the public and the scientific community, and the aura of mystery enshrouding the species began to clear. To everyone's surprise, he proved to be gentle, inquisitive and cooperative, not at all like the ferocious beast of repute. Moby Doll captured the public's fascination, and soon there was great interest among aquaria to display the fabled killer whale. The following year, 1965, another killer whale was captured by fishermen near the town of Namu on the central BC coast. The adult male was purchased for $8,000 by the Seattle Aquarium and towed 700 kilometers in a floating pen to Puget Sound. This whale, named "Namu" after his place of capture, became even more famous than Moby Doll, and was featured in National Geographic articles, books and TV documentaries. To satisfy demand for killer whales in aquaria, a commercial live-capture fishery for killer whales grew quickly in both southern BC and Washington State. By 1973, 48 animals were captured and transported to aquaria around the world and an additional 12 died during the capture operations. The fishery was lucrative for the whale hunters, with the price quickly rising to $70,000 per animal by 1973.

By 1970, public concern about the effect of this fishery on local killer whales was mounting, something that would have been most unlikely a decade earlier. There were no controls on the fishery in BC or Washington State, and people began to worry that killer whale numbers were being depleted. Opposition was also growing to the escalating harassment the whales were receiving as they were becoming increasingly difficult to corral into bays where they could be netted. Although the pubic was becoming more familiar

Live-captured killer whale, Pender Harbour, BC 1968. Photo courtesy of the Vancouver Sun

with killer whales from seeing them in aquaria, there was still no scientific information with which to manage this fishery – basic biological parameters such as population structure, abundance, and birth and mortality rates were not available.

In response to this concern, in 1970 the Canadian Department of Fisheries and Oceans (DFO) tasked a young marine biologist, Dr. Michael Bigg, with providing advice on how to manage this live-capture fishery. Mike Bigg had recently completed graduate studies at the University of British Columbia, studying harbour seals in coastal BC, and had taken a position as marine mammal scientist based at DFO's Pacific Biological Station in Nanaimo, BC. His first approach to this assignment was to develop a public sighting program to determine roughly how many killer whales were



Poster promoting the annual sighting census in British Columbia and Washington State, 1973.

in the region and where they could be reliably found. During 1971–73, Bigg and his co-worker Ian MacAskie distributed about 15,000 sighting forms each year to fishermen, mariners, lighthouse keepers, and others who lived or worked along the BC coast. Bigg realized that with such an intensive sighting program, multiple sightings of the same groups could become a problem for censusing the population. To get around this complication, they focused effort on a particular weekend during the summer each year, so that potential duplicate sightings of the same animals could be determined from the time of the report and the group's direction of travel and removed from the analysis. About 500 sighting forms were returned each year and from these Bigg estimated that there were roughly 200–350 killer whales in coastal BC and Washington State. This was far fewer than originally thought, and suggested that the live-capture fishery could be having a population-level effect. The sightings program also revealed two "hot spots" for killer whales on the coast – Johnstone Strait off northeastern Vancouver Island and Haro Strait, the transboundary channel between the US San Juan Islands and southeastern Vancouver Island.

To observe the whales firsthand, Mike Bigg and Ian MacAskie conducted a boat survey of Johnstone Strait in the summer of 1972. Also observing the whales in this area was Dr. Paul Spong, a psychologist who had previously undertaken studies of captive killer whales at the Vancouver Aquarium in the late 1960s. As Bigg and MacAskie observed and photographed the whales, they noticed that several had highly distinctive dorsal fins, apparently resulting from old wounds that had healed. Some of these whales were given nicknames according to their fin's features, such as "Stubbs," who had lost the top portion of her fin, and "Nicola," who had a distinctive nick at the top of the fin. The following year, Bigg and MacAskie returned to Johnstone Strait and not only did they relocate these distinctive whales, they discovered that every individual bore unique markings – nicks and gouges on the dorsal fin and scars and pigmentation patterns on the saddle patch at the base of the fin. Bigg realized that these "natural tags" could be used to reliably recognize each animal, and the focus of their field studies shifted to photographically identifying and tracking individual whales.

This novel photo-identification technique was considered quite radical and unproven at the time, but Bigg persisted despite skepticism from some established cetacean biologists. He was convinced that photo-identification was the key to answering many of the important questions about killer whale life history and population dynamics. To help demonstrate the permanence of fin markings, in October, 1973, Bigg had a veterinarian surgically incise two V-shaped notches in the dorsal fin of an adult male killer whale that was temporarily held captive at Pedder Bay, west of Victoria,

"Stubbs" lost the top portion of her fin, becoming easily recognized as Bigg and MacAskie conducted their photographic survey. Photo by Ian MacAskie

K1 helped prove the permanence of fin markings for identification. Photo by Ken Balcomb

BC (these notches were still unchanged when the whale, K1, was last seen in 1997).

In 1974 and 1975, Bigg's study was expanded to include coastal waters from southern Vancouver Island to Fitz Hugh Sound north of Vancouver Island. Graeme Ellis, a young whale enthusiast who had been in Johnstone Strait observing and photographing killer whales in 1973, joined the study team. With the promotional help of newspapers, radio, and marine broadcast stations, they developed an extensive network of volunteer whale spotters who telephoned a central hotline when killer whales were seen. Upon receiving a call, they immediately dispatched a boat and crew to intercept and photograph the individuals. This technique worked well – by late 1975, they had logged around 300 encounters with killer whales and some important findings were beginning to emerge.

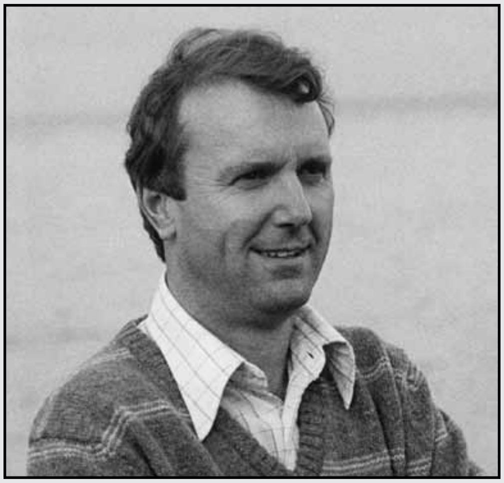
Early in this field effort it became clear that killer whales usually travelled in stable groups composed of the same individuals. To keep track of these pods and their members, Bigg and co-workers assigned a letter name to each group as they were encountered, and a number to individuals in the order in which they were identified. Thus, A1 was the first individual identified in the first pod, A2 the second, and so on. As chance would have it, the first encounters in Johnstone Strait were actually with a temporary aggregation of three pods, so the initial "A pod" was split into three pods that were each named after the most distinctive individual in the group – hence A1, A4 and A5 pods.

As Bigg and Co. made their way through the alphabet, they quickly became familiar with many of these pods and their members. These typically comprised 10-25 individuals of both sexes and all age classes, including one or more mature males and calves. With such demographics, it appeared that these pods were likely breeding units, with the adult males having sired the calves in the group. As these pods could be found frequently and predictably in certain location, especially during summer and fall, they were considered residential in the area and were termed "residents." Two communities of resident pods were identified, a northern community in Johnstone Strait and waters to the north, and a southern community off southern and eastern Vancouver Island. Pods within each community frequently mixed and travelled together, but the two communities appeared socially isolated even though their ranges overlapped somewhat.

On rare occasions, Bigg and his team encountered killer whales that did not seem to belong to these communities. These were in small groups of less than six individuals that were mostly found in unusual locations where residents were seldom seen and they were not observed to mix with the resident pods. As they were unpredictable and erratic in their movements, Bigg and co-workers reasoned that these were likely in transit through the range of the resident communities, and thus they called them "transients." They were unsure what to make of these transient pods, but it seemed likely that they were composed of individuals that had dispersed from the larger resident pods and that they might ultimately group together to form their own resident-type pod. Their behavior patterns resembled the "low-profile" behaviors of lone wolves when moving through a pack's territory.

In early 1976, Bigg, MacAskie and Ellis summarized their results in a technical report and provided advice for managing the live-capture fishery. Their photo-identification studies had resulted in a population census of about 275 whales, consistent with their earlier estimate from sighting reports, and this small population clearly could not support the number of removals seen in the late 1960s and early 70s. They remarked that "...it is important to recognize the

Bigg's Killer Whale: A Tribute to the Man Who Started It All



Dr. Michael A. Bigg 1939-1990

Those of us who study wild killer whales today owe much to the pioneering and visionary work of the late Dr. Michael Bigg. In the early 1970s, Mike was faced with the challenge of determining the status of killer whales in coastal waters of the Pacific Northwest for the Canadian Department of Fisheries and Oceans – at that time, almost nothing was known about the species, either in that area or elsewhere. Early in his study, Mike devised a novel field technique for studying the species – photographic identification of individuals using natural markings. This was a radical approach and some questioned whether it was even possible. While most agreed that some well-marked whales could be recognized and followed, it was Mike's discovery that *every* individual was identifiable with a high quality photo that made the difference. Mike proved beyond any doubt that photo-identification is the key to understanding the lives of killer whales, and it is now the standard tool used in field studies of killer whales globally.

For over 15 years, Mike documented in meticulous detail the demographics and dynamics of killer whales in coastal waters of the Pacific Northwest – births and deaths, social associations of individuals and pods, and many other aspects of their natural history. What is most astounding is that the majority of this ground-breaking work was done in his spare time, as Mike's official research priorities were seals and sea lions (and his research on those species was impressive as well). Mike was driven by a passion to solve the mysteries of killer whale life history, and his enthusiasm was infectious. He loved to share in the excitement whenever new insights were gained, and he inspired and encouraged many students and research colleagues to undertake studies of their own to better understand this remarkable animal. Mike's office at the Pacific Biological Station on Vancouver Island became a mecca for students from around the world, who would come for advice about how to study these animals in the wild. Always free with his time and knowledge, Mike made sure that they headed off on the right path.

Of all the interesting facets of killer whale life history, Mike was particularly fascinated by the relationship between "residents" and "transients." The notion that two different forms of killer whale could coexist in social and reproductive isolation, each with its own distinct diet and lifestyle to match, was without precedent and hard to explain. How could this situation have evolved and how was it maintained? Mike pondered such questions at length, discussing ideas with colleagues and writing copious notes summarizing his thoughts. Sadly, Mike was never able to write up his studies on transient killer whales – he died of leukemia in 1990, at the age of 51.

Over the two decades that have passed since Mike Bigg's death, much has been learned about killer whales in different parts of the world. It is now clear that distinct, ecologically specialized populations coexist in other regions as well, and may be typical of killer whales globally. How killer whale ecotypes might have developed and what they represent from an evolutionary perspective are hot topics in the current scientific literature on cetaceans. Central to the recent discussion on potential speciation of different killer whale lineages that share the same waters are ideas that Mike had been deliberating on over 25 years ago, as his unpublished notes from 1985 reveal: *"With a high degree of intelligence (i.e., flexible behavior, not all instinctual) and long lives, differences in behavior and morphology can develop within separate lineages that are sympatric. This is possible because the social isolation of each lineage […] in killer whales appears to be so complete as to function in a manner equivalent to geographical isolation."*

The body of evidence that transient killer whales represent a distinct species from other killer whales lines is becoming compelling. Although it may take some time before this is resolved and a new species is formally proposed, there is a growing movement among killer whale researchers that transient killer whales be called "Bigg's Killer Whale." This would indeed be a fitting way of honoring the memory of this remarkable pioneer of killer whale science. – J. F.

Transient groups, originally thought to be small outcast groups from resident pods, were later shown to be an entirely distinct form of killer whale. Photo by Mark Malleson

high esthetic and recreational value which many people from British Columbia and Washington place on seeing killer whales in the wild...” and recommended that if any future live captures were to be permitted, they should be limited to the replacement of existing animals in Canadian aquaria. However, by this time public sentiment was strongly opposed to the captures in both Canada and the US. Finally, outrage triggered by the chasing, corralling and capture of a small transient group at Budd Inlet, near the Washington State capitol at Olympia, in March 1976, brought an end to the commercial killer whale fishery in the region.

With this primary management assignment completed, Mike Bigg was given new research priorities and the killer whale field program was scaled back. But Bigg had become fascinated by killer whales, and he felt that the study had only begun to shed light on the many unanswered questions about their life history and behavior. The social structure of the resident pods was still unclear, as was their relationship to the transient pods that periodically lurked in their range. He had some preliminary estimates of recruitment rates in the resident pods, but good data on natural mortality and birth rates and other life history parameters were needed to better understand their population dynamics. Another major gap was the feeding ecology of the whales – it was long suspected that killer whales in the region preyed on a variety of marine mammal and fish species, but most evidence was indirect and anecdotal. Bigg and his team had collected prey fragments – mostly salmon scales – from a few feeding events, but details of the whales’ diet were mostly lacking.

Although Bigg was able to continue some killer whale field work, his resources were insufficient to tackle these important questions. Fortunately, new researchers started joining the effort. In the summer of 1976, cetologist Ken Balcomb began Orca Survey, a field study of killer whales in the San Juan Islands and Puget Sound, with initial support from the US National Marine Fisheries Service. Balcomb’s long-term study was also based on individual photo-identification, and he worked closely with Bigg to ensure standardization of field methodology and whale naming protocols. Balcomb’s team soon expanded to include students Jim Boran, Sara Heimlich, and Rich Osborne, who later turned their results into graduate theses. In 1977, I began a field study of the acoustic behavior of killer whales around Vancouver Island, working as a graduate student at the University of British Columbia and as a member of the Bigg team. Since much of this research involved describing and comparing the vocal repertoires of different pods, photo-identification was central to my field studies as well. Another graduate student, Jeff Jacobsen, from Humboldt State University in California, began field research on behavior of northern resident killer whales in 1979. Jacobsen contributed his identification photos to the study, as did University of California Santa Cruz graduate student David Bain, who studied northern residents during 1981-86.

Thanks to this collaborative effort, field studies continued without interruption and complete annual censuses of the resident population were possible. Over time, many of the gaps in our understanding of the life history and behavior of Pacific Northwest coast killer whales began to be filled. Some of these findings were totally unexpected, and forced a complete revision of the early thinking about residents and transients. Transients turned out not to be social outcasts from resident pods, but instead were found to be an entirely distinct form of killer whale that differed from residents in social organization, behavior, vocal patterns and, most importantly, diet. Transients feed on marine mammals and the occasional sea bird, and residents on salmon and other fishes. The structure of resident society was revealed to be unlike that of any other mammalian species – pods are composed of close kin that are all descendants of a common maternal ancestor, and individuals appear to stay within their natal group for life. Residents have long lifespans, with females living 50 years on average and some living to 80-90 years. Pods can thus contain matrilines with up to four generations of living whales. Residents also have a complex system of vocal dialects that are without precedent in other mammals. Pod-specific calls seem to encode information on maternal genealogy and may be important for group cohesion and inbreeding avoidance. These findings, as well as many others too numerous to list, were only possible due to the long-term and collaborative nature of this study.

As field studies continued into the late 1980s, the story of the population dynamics and social organization of resident killer whales was becoming clearer and Bigg began putting together two key manuscripts describing these findings. There was a new urgency to completing this work, as he had recently been diagnosed with leukemia and the outlook was not promising. With the assistance of his quantitative colleague Peter Olesiuk, the complicated data analyses were completed and Bigg was able to finish these manuscripts in time to see them in print before he died in 1990.

What began as a short-term management-focused task had, by the time of Bigg's death, evolved into an on-going multi-disciplinary study that was investigating diverse facets of killer whale biology in ever increasing detail. This study is now approaching its fifth decade and, in addition to Bigg's long-term friends and colleagues, it has involved dozens of younger researchers and students. This research has and continues to yield surprising new discoveries, many of which have only been possible due to recent advances in field methods and technologies.

One discovery that none of us anticipated was the existence of yet another distinct form of killer whale sharing Pacific Northwest coastal waters with residents and transients. The first evidence of this population were some snapshots taken in 1988 by ecotour operators and passengers in waters around Haida Gwaii, formerly known as the Queen Charlotte Islands. These islands are located on the continental shelf edge about 200 km northwest of Vancouver Island and 75-100 km off the mainland coast of British Columbia. None of these whales were familiar to us, but judging from the large group sizes they were likely unidentified pods from a different resident community. It wasn't until we started doing field work in Haida Gwaii and on the offshore banks of the west coast of Vancouver Island in 1990 that we began to encounter and work with these whales ourselves. It quickly became apparent that these whales were quite unlike residents and transients – their fins were more rounded with significantly more nicks and gouges, the whales appeared somewhat smaller than the other types, and their underwater calls were different from any known dialect. Since they were found on the continental shelf beyond the exposed outer coast and had not been seen in protected inshore waters despite almost 20 years of study effort, we started calling them "offshore killer whales."

Our understanding of offshore killer whales slowly improved over the 1990s and early 2000s. Colleagues began photographing the same individuals as far south as southern California in winter and as far north

Compared to residents and transients – offshore killer whales are smaller and their fins are more rounded, often with nicks along the trailing edge. In addition, they regularly slap their tails when they are swimming and their vocal dialect is unique from other known dialects. Their conservation status is somewhat uncertain, and they have been recently uplisted from "Special Concern" to "Threatened" in Canada. Photo by Paul Wade, Alaska Fisheries Science Center as Kodiak in summer, suggesting a broad seasonal movement up and down the outer coast. But how offshores compared ecologically to residents and transients remained unclear. A clue that their diet differs fundamentally from that of the other ecotypes was the extreme wear of their teeth. Although only three stranded offshore whales were available for examination, the teeth of all three were worn flat to the gums, something that is never seen in residents or transients. This suggested that the diet of offshores is dominated by prey that is far more abrasive than the salmonid and mammalian prey of residents and transients. We speculated that they may specialize on sharks, since the skin of sharks is so roughened by embedded denticles that it was used historically as sandpaper. It wasn't until very recently that we and our Alaskan colleague Craig Matkin were able to document multiple predation events by offshores in northern BC and Prince William Sound, Alaska. These kills took place at depth and the only evidence of feeding were pieces of shark liver floating to the surface. We collected samples from numerous kills and, thanks to DNA analysis, they were identified as Pacific sleeper sharks, a large (to at least 4.4 m /14 ft.) deep-water species quite common along the continental shelf of the northeastern Pacific. Although there is much more to learn about the foraging strategy of offshore killer whales, it appears that they are indeed an ecotype distinct from residents and transients.

Advances in molecular DNA analysis techniques have been instrumental in clarifying the genetic relationship of residents, transients and offshores. In the late 1980s, graduate student Tracy Stevens of Portland State University analyzed mitochondrial DNA from captive and stranded whales and provided the first evidence that residents and transients are genetically distinct. This was later confirmed with a larger sample size by geneticist Russ Hoelzel and colleagues, who were also able to put residents and transients in a broader context with samples from other ocean regions. Researcher Lance Barrett-Lennard, as a PhD student at the University of British Columbia, greatly advanced our knowledge of both killer whale population structure and mating patterns through extensive DNA analyses. He showed that offshores are genetically distinct from both residents and transients, though they are more closely related to residents. Using nuclear DNA, Barrett-Lennard also provided evidence that these different ecotypes rarely if ever interbreed, as was long suspected due to their social isolation from each other. With DNA fingerprinting techniques, he also found that adult males don't start fathering offspring until they are well into their 20s, and that they mate preferentially with females outside their pod, especially those within their population having vocal dialects that are the most unlike their own. This supports the hypothesis that dialects serve as more than acoustic family badges – they help reduce the risk of inbreeding in these kin-structured societies. Most recently, Phillip Morin and co-workers used the latest mitogenomics techniques to show that transients likely began diverging from residents and offshores over half a million years ago, and they suggest that this warrants transients being considered as a distinct species.

Mammal-eating killer whales commonly subdue their prey, even large whales, by ramming them repeatedly; here a Dall's porpoise is sent flying. Photo by Jared Towers

The photo-identification technique, together with the unusually closed social structure of resident killer whales, have facilitated highly accurate annual censuses of both northern and southern resident populations since the early 1970s. Although it was long recognized that these populations were very small and were impacted by the earlier live-captures, they were slowly but steadily increasing in abundance during the 1970s through early 1990s. As a result, there was little urgent concern regarding their conservation status. This complacency ended suddenly in the mid 1990s, when both southern and northern resident populations began to decline sharply. As these declines continued through the late 1990s, new findings were coming to light that provided a possible explanation. First, resident killer whale foraging is highly focused on Chinook salmon, and the smaller but far more abundant species such as pink and sockeye salmon are not significant in their diet.

As many Chinook salmon stocks were well below their historical abundance, perhaps food supply was playing a role in the declines. Second, toxicologist Peter Ross was finding extremely high levels of PCB contaminants in blubber samples collected from residents by Barrett-Lennard and co-workers. These levels were potentially sufficient to cause a range of impacts on the whales' health. As a result of these new conservation concerns, the southern and northern resident populations were listed as Endangered and Threatened, respectively, in Canada in 2001, and southern residents as Endangered in the US in 2005.

Fortunately, the declines in the resident populations ended in the early 2000s, and since then northern residents have been steadily increasing in abundance while numbers of southerns have been roughly stable. Our research has shown that the declines of the late 1990s were driven by unusually high mortality rates that were spread throughout both populations and most age and sex classes. A comparison of resident survival rates to coast-wide Chinook salmon abundance over a 25-year period revealed a highly significant correlation, suggesting that resident populations may be limited by this one key prey species. On this weight of evidence, fishery managers in both Canada and the US have started working with whale biologists to help ensure sufficient availability of Chinook salmon stocks in areas and at times of importance to resident killer whales.

Transient killer whales were listed as Threatened in Canadian waters in 2001 due to their small population size and high concentrations of organochlorine contaminants in their blubber. PCB levels are much higher than those seen in residents due to greater bioaccumulation of these contaminants in the marine mammals fed upon by transients. Although contaminants are a concern, transient killer whales in the Pacific Northwest appear to be doing very well and increasing in abundance, likely because the abundance of their primary prey, harbor seals and sea lions, has increased dramatically over the past four decades. The status of offshore killer whales is somewhat uncertain, and they have been recently uplisted from 'Special Concern' to Threatened status in Canada. Despite its extensive range along the continental shelf, the population appears to be quite small, probably fewer than 500 animals. A better understanding of the diet of offshores is needed in order to assess the status of prey populations and how they may be affected by human fisheries.

Killer whales, such as this southern resident, have surprisingly good vision out of the water and often "spyhop" to take a look around. Photo by Dave Ellifrit, Center for Whale Research

Almost 40 years have passed since Mike Bigg pioneered the use of photo-identification to study killer whales in the Pacific Northwest. As a result of his efforts and those of dozens of research colleagues and students, we have gained a remarkable amount of knowledge about these animals. The resident killer whale populations of the Pacific Northwest are now among the best known of any cetaceans, rivaled only by the bottlenose dolphins of Sarasota Bay, Florida. Today, more than 80% of the individuals in these resident populations were born since the photo-identification study began and population genealogies, demographics and dynamics have been documented in great detail. In time, all the whales in these populations will have been followed since birth, and the potential to learn from them will only increase. Hopefully, the iconic status of killer whales to people of the Pacific Northwest will continue to provide the impetus to protect them and their habitat for years to come.

Killer Whales In Alaskan Waters

by Craig Matkin and John Durban

Fish-eating "resident" killer whales frequently interact with fishing vessels in Alaskan waters, often helping themselves to discarded fish or even the catch. Photo by Dave Ellifrit, North Gulf Oceanic Society

Craig spent his undergraduate days roaming California with the renowned cetologist Ken Norris, so it was natural that killer whales grabbed his attention thirty-five years ago when they first surrounded his kayak in Prince William Sound. Working in the remote western Sound as a fisheries biologist, he was surprised and fascinated by his many encounters with killer whales, leading him to switch his focus to a long-term study of their population biology in Alaska. John began to work in Alaska ten years ago, leading NMFS field studies investigating the predatory impact of killer whales on endangered marine mammals, specifically Steller sea lions. Although an accurate picture of killer whale diet and predatory impacts is still emerging, these long-term and recently intense studies have gathered a wealth of information on Alaska's killer whales, which is informative in both a local and worldwide context. All three eastern North Pacific killer whale ecotypes are found here in Alaska, the fish-eating "residents," marine mammal-eating "transients," and shark/fish-eating "offshores." Some Alaskan waters, such as Prince William Sound/Kenai Fjords and particularly the waters of the Aleutian Islands and Bering Sea shelf edge, have some of the highest densities of killer whales in any of the world's oceans.

It is the resident ecotype that is found in the greatest numbers in Alaska, reflecting the relatively healthy stocks of salmon and other fish. We have over 700 individual resident killer whales photographed and catalogued in the waters stretching from southern southeast Alaska to Kodiak Island and over 1,500 from the Aleutian Islands and Bering Sea shelf edge (and we are still discovering more with every field effort!). As in Washington and British Columbia, residents appear to travel in pods that are made up of stable matrilines (a female and her offspring – both male and female), making it possible to accurately track the numbers of whales in areas where there are regular photo-identification programs. Overall, the numbers of resident killer whales in southeastern Alaska and the northern Gulf of Alaska has been increasing at rate of over 3% per year over the past 25 years, except for the whales involved in the Exxon Valdez oil spill in 1989. In great part this is likely the result of the rebound of salmon stocks throughout the region.

In the Gulf of Alaska, which includes our primary study sites in Prince William Sound and Kenai Fjords, resident killer whales are dependent on salmon for sustenance during spring, summer and fall; but not just any salmon. They seek out primarily the fatty Chinook and Coho salmon, some chum salmon, and little or no sockeye or pink salmon. In western Alaska, where the resident killer whales are likely a separate population, salmon are much less abundant, and they may feed on other fish species, such as Atka mackerel; however, we have little feeding data from this region. It is also around the

Aleutians and Bering Sea that longline fishermen have the greatest problem with abundant resident killer whales that remove black cod, halibut, and turbot from hooks on their lines. This depredation has been occurring for decades, and the high abundance of resident killer whales in this region may be at least partly due to year-round "provisioning" with fish from longlines. Depredations are not limited to this region, the smaller Prince William Sound blackcod longline fishery also has had repeated trouble with killer whales. Some groups of resident whales in western Alaska (that we have dubbed "trawler trash") also line up to eat the rich bycatch and unwanted fish that are dumped off the decks of the trawlers.

The fish-eating resident pods most frequently seen in southeastern Alaska (AG, AF5 and AF22 pods) also make regular, but unpredictable trips across the Gulf of Alaska to Prince William Sound and Kenai Fjords. These forays occur in both summer and winter and may extend as far west as Kachemak Bay and the Alaska Peninsula, over 1000 km (621 miles) from their home grounds. So much for the notion that resident whales are tied to one locality! Oddly, none of the resident pods regularly encountered in Prince William Sound have ever been seen in southeastern Alaska. The travel of southeastern Alaska pods is likely related to the potential to socialize and breed with more distantly related pods. And Prince William Sound/ Kenai Fjords seems to be a central meeting place for pods that range from southeastern Alaska to near the Shumagin Islands off the Alaska Peninsula. When the AX pods that primarily range around Kodiak Island and the AW pod from the Shumagin Islands area all meet in Prince William Sound there may be 10 or more pods and 150 or more whales all feeding and socializing together. Although these "superpod" encounters seem more common in late summer, they may occur at other times from June through October. Keeping track of the individuals in these mixed groups, by scrutinizing the fins and saddle patches is enough to make your head spin. Listening with hydrophones isn't any less confusing, but it gives a strong indication of the level of social activity and communication that is occurring. Since each pod has its own vocal dialect the variety of calls is astounding, especially when mixed with the excited social calls and whistles that occur during these aggregations. It is likely that these vocal dialects and calls allow the whales to sort each other out as well and find distantly related whales to mate with. The more distantly related the whales are, the more different are their vocal dialects.

In Prince William Sound we were able to track the fate of the major resident pods before, during, and after the Exxon Valdez oil spill. We watched as AB pod, which lost 13 out of 36 individuals following the spill, traveled through passages full of oil and oil sheens days after the spill, sometimes surfacing in it. The deaths changed the social structure of the pod; many females that led matrilines were lost, reducing their ability to recover. This apparently caused the pod to split, and 20 years later they are not fully recovered from the spill and still travel as two separate pods.

Another small population of transient whales, the AT1 group, lost 9 of 22 members following the spill, and has produced no new offspring in the two decades since. It will likely die out as only seven AT1 whales remain. This small, genetically and acoustically unique group may have been in decline prior to the spill, but the oil spill sealed its fate. The AT1s specialize in surprising seals along the rocky shorelines of Prince William Sound and in cornering the fast-swimming Dall's porpoises in deep-water areas. Hunting the hundreds of seals that regularly haul out on ice floes in front of glaciers is another place you will find them. The AT1s seem as much a part of the waters of Prince William Sound and Kenai Fjords as the glaciers and rocky shorelines, and it is difficult to imagine the day when there will no longer be the possibility of being surprised by their sudden appearance.

The AT1 transients are one of those unique biological finds, that both puzzle and amaze biologists. Another unique twist to the Prince William Sound transient story, however, is the occasional presence of another, more widespread population of transient killer whales, called the Gulf of Alaska (GOA) transients. These transients are widely dispersed and infrequently seen, and we have identified less than 100 individuals although photographic recapture analysis suggests a stable population. It is a unique situation to find two transient populations that do not associate or interbreed, swimming regularly in the same waters. GOA transient individuals have been seen from southeast Alaska to the Shumagin Islands. On rare occasions, GOA transients are photographed in the inside waters of southeast Alaska and northern British Columbia. Once they were seen mingling with another discrete transient population, the West Coast (WC) transients.

The WC transients have been steadily increasing during photo-identification studies over the past 40 years and appear to number about 260 individuals across their range from northern Southeast Alaska south to Washington State. We estimate the density of WC transients in British Columbia to be nearly 18 times that of GOA transients in Kenai Fjords/ Prince William Sound. This probably has much to do with trends in harbor seal and Steller sea lion populations over the past forty years; increasing in British Columbia and southeast Alaska compared to a big decrease in the northern Gulf of Alaska.

Certainly the most challenging mammal prey for transient killer whales are the baleen whales. The smaller minke whales and migratory gray whales seem the favored species in Alaska, although we recently recorded predation on humpback whales and suspect there is a group of killer whales around Kodiak Island that specialize in preying on the steadily increasing population of humpback whales.

Our most dramatic and consistent observation of predation on whales has been at the western end of the Alaskan Peninsula, near Unimak Pass, where migrating gray whales cross a shallow-water shelf as they make the turn northwards into the Bering Sea. This is a gathering ground for 100 or more transient killer whales each spring that come to intercept the grays. Essentially all of the shore-hugging gray whales that complete the migration to the Bering Sea must run this gauntlet. Since the waters are shallow, when a gray whale is killed and sinks (as they generally do), it remains within easy depth for the killer whales to return and feed on following days. The lips and tongue are the most tender and prized parts of the whale and these parts alone are more than enough food to fill the three to seven whales that generally make the kill. So the bulk of the whale remains uneaten after the initial gorging, but is generally revisited by the whales that killed it, or is fed upon by other killer whales roaming the area, and by Pacific sleeper sharks that take bowling ball-sized bites out of the carcass.

A sunken carcass may seep oil for days, and it can provide a nicely marked location for us to “stake out” and intercept the returning killer whales. However, if a whale is killed close to the shore and does not sink immediately, it may be washed up on the beach where it becomes not only food for brown bears, foxes and other wildlife, but provides clear “evidence” that the killer whales preferentially eat the lips and tongue. In reality, if the carcass were to remain accessible the killer whales would likely return to feed again on other parts of the whale, or another group of killer whales would move in and feed. Little of the beached carcasses are wasted, as the brown bears take full advantage of the windfall and clean the carcass down to the bones with help of the abundant foxes. These massive bears patrol the beaches looking for bits of blubber at this time of year: we have watched them run to the

A sub-adult male transient killer whale attacks a juvenile gray whale as it migrates around the western end of the Alaska Peninsula. This annual aggregation of killer whales represents a significant threat of mortality to young gray whales. Photo by John Durban, North Gulf Oceanic Society beach in anticipation when the killer whales make an attack along the shore.

Our initial assumption was that killer whales were so agile and strong that they could simply rip into the flesh of a living gray whale with their powerful jaws, making short work of dispatching the whale. This has proven not to be true. A gray whale is typically drowned by holding it beneath the surface before substantial chunks of flesh are removed. This is no small feat, but the gray whale skin and blubber is extremely tough and difficult to rip into, and much easier to accomplish if the whale is dead. If the target is a calf, as they mostly are, it must first be separated from its mother. This can also be a very difficult process as the killer whales are very cautious near an agitated, fluke-slashing gray whale cow, and it is the prowess of gray whale mothers that keep most calves safe. The gray whales will also seek shallow water when pursued by killer whales; if the water is shallow enough the killer whales cannot drown them. Also, the killer whales will not risk injury from being crushed on the bottom by thrashing gray whales. We have watched killer whales pushing gray whales backwards by latching on to the front of the pectoral flippers to keep them out of the shallows. To avoid this, gray whales will spiral on their long axis, to make their pectoral flippers less accessible. We have also seen gray whales strand themselves temporarily to avoid drowning by killer whales.

The killer whales take mostly calf gray whales, but also small juveniles. If about 60% of the carcass is actually consumed by killer whales, then 100 calves and 20 juvenile grays would be needed to satisfy the estimated feeding requirements of the killer whales that we see there during the five weeks of most intensive activity. In some years this might have a significant impact on the calf production since calves comprise 1-8% of the population of about 20,000 gray whales. On a given year, in this region alone, killer whales may remove anywhere from 5-50% of the calf production.

Our tagging with satellite LIMPET tags suggests that some of these killer whales remain in the area after the bulk of the gray whales have passed, but most scatter across the Bering Sea. Some appear to follow the gray whales northward along the coast into the northern Bering and Chukchi Seas. One killer whale group traveled 1400 km (870 miles) north in eight days, right up to the ice edge north of the Bering Strait. None of the transient killer whales from the Unimak Pass area have been recorded east and south into the Gulf of Alaska, or further west along the Aleutian Islands. All this suggests that the western end of the Alaska Peninsula is a gathering ground for killer whales that at other times range over a wide areas of the Bering Sea, or perhaps pelagic waters of the North Pacific Ocean.

Questions and debate still surround the extent and impact of transient killer whale predation on endangered Steller sea lions. Photo by Dave Ellifrit, NOAA Alaska Fisheries Science Center, NMFS Permit No. 782-1719

Another area where transient killer whales time their arrival with the migration of prey is the Pribilof Islands where thousands of Northern fur seals arrive in spring to pup and mate. The arrival of the fur seals in late May and June, coincides with the appearance of small groups of transient killer whales that focus on consuming fur seals. Much of the predation occurs within a few miles of rookeries, particularly in the evenings when the fur seals leave to feed offshore, and early mornings when they return to the rookeries. The primary target in this early season seems to be the juvenile and young adult males – these are among the largest of the seals with the highest fat content, preparing them to wait for several weeks in an attempt to access prime real-estate on breeding rookeries… and hopefully attract a harem. However, they are typically out-competed by the larger adult males and settle for sub-optimal breeding opportunities in the water around the rookeries. This exposes them to predators.

The transient killer whales operate in small groups and often seem to ignore the more abundant female fur seals, until suddenly a chase occurs, followed by breaching. Quickly a fur seal is dispatched, although sometimes juvenile whales seem to "play" with it before it is consumed, repeatedly whacking the hapless fur seal with their flukes. This may also serve to immobilize the fur seal, whose sharp teeth represent a potential danger to killer whales. The whales typically wander off to rest and socialize away from the islands during the middle of the day only to circle and return at dusk to hunt again. Although only around 50 individual transients have been identified around these islands, many of the same whales are seen repeatedly during the season and over the years. The whales seem to leave the islands by early July although the abundant fur seals remain apparently available, but return in fall, presumably to take the pups that are leaving the rookeries. A few of these Pribilof whales have been seen at other times in the Aleutian region, but genetic analysis of biopsy samples connects most of them with transients on the Russian coast of the Bering Sea. Just what they do when the leave the Pribilofs is not certain, but there is no doubt they travel substantial distances. One satellite-tagged whale headed southward more than 1800 km (1120 miles) into the subtropical transition region of the central North Pacific, nearly halfway to Hawaii.

In the last decade or so, Alan Springer, Jim Estes and colleagues have repeatedly suggested that transient killer whales have been eating their way down the food chain, causing a sequential megafaunal collapse of seals, sea lions and sea otters in Alaskan waters. Although there has been much disagreement and debate about the evidence for this hypothesis, it has inspired intense research into the current extent and impact of killer whale predation on endangered marine mammal species, specifically Steller sea lions and sea otters. Our photographic mark-recapture analyses estimated that approximately 350 transient killer whales currently use the coastal waters around haulouts and rookeries of the endangered western stock of Steller sea lions in the western Gulf of Alaska and Aleutian Islands. Energetic models suggest that this is more than enough killer whales to cause the observed declines of sea otters and sea lions, if they focused their predation on these species. However, this specialization does not appear to occur. Instead, our observations suggest some seasonal specialization (e.g., gray whales at migration time, or fur seals at breeding time). Furthermore, stable isotope analysis of skin biopsy samples has shown that the spring/summer diet of transient killer whales in the Aleutian Islands is not composed exclusively or even primarily of Steller sea lions or sea otters, a finding supported by field observation data indicating that gray whales, minke whales, and northern fur seals comprise a substantial portion of the their diet. Additionally, transient killer whales sampled in the Bering Sea have stable isotope signatures consistent with a largely cetacean diet (e.g., Dall's porpoises, minke whales, and gray whales). We have not observed actual consumption of sea otters in this region, although there are a few accounts from other researchers.

An adult male transient killer whale photographed in the Central Aleutian Islands, with dark oval scars on the saddle patch, which are the healed bites from cookiecutter sharks. These small sharks only occur in warm, offshore waters, and these scars therefore imply movements to tropical or sub-tropical Pacific Ocean waters. Photo by Dave Ellifrit, NOAA Alaska Fisheries Science Center, NMFS Permit No. 782-1719

Additionally, it doesn't appear that transient killer whales spend all (or perhaps not even the majority) of their time in near-shore waters where Steller sea lions or sea otters forage. Transients photographed around the Aleutian Islands and in Bering Sea typically have oval scars on their bodies, caused by bites from small cookiecutter sharks that live only in warm, deep and pelagic waters of the tropical and sub-tropical oceans. This indirect evidence of movement away from cold Alaskan waters has been supported by direct evidence from satellite telemetry. Three whales tracked with satellite tags (including two tagged in the central Aleutian Islands and one previously mentioned from the Pribilofs) moved rapidly away from Alaskan waters, south into sub-tropical waters of the central North Pacific. It is currently not clear how frequent these movements are, or the proportion of time whales spend in those pelagic waters, but it is clear that these transients are not always present to prey on coastal marine mammals in Alaska.

Some Gulf of Alaska transients do appear to specialize in preying on Steller sea lions at times. In Kenai Fjords, a female we named "Matushka," traveled alone for years after her son died. She made regular visits to the Chiswell Island Steller sea lion rookery when the new pups started entering the water. The bellowing of the agitated sea lions could be heard from miles away when they spotted her fin or when she was able to grab an adventurous pup. Later she joined with another female whale that produced a new calf. The Chiswell rookery became a training ground for the youngster, although they started him out on puffins and cormorants. After the adults stunned an unsuspecting bird with their flukes, the yearling whale would come in and practice its fluke slaps and carry the bird in its mouth until it vanished or was left maimed at the surface. Although occasionally reported as prey, sea otters don't seem to be preferred by GOA transients, but provide an excellent opportunity for training young whales. They may be abandoned alive after training is over. Learning to handle mammal prey appears a serious business that requires gradual training steps.

Although offshore killer whales are much less frequently encountered in Alaska than the other ecotypes, their appearance is often dramatic when they arrive in fast-moving groups of over 100 whales. Physically, they appear a bit smaller and seem quicker than other North Pacific killer whales and never seem to stop moving or changing traveling companions and groups. When feeding they may have long dive times of 5 minutes or more and appear to be deep divers. The limited tagging data we have for them also indicates they travel faster and over greater distances each day than do residents or transients. Tracklines show them spending time out on the shelf break in our area, which may be 80 km (50 miles) or more offshore, with forays to inshore waters. Tagging data also indicates 125 km (78 miles) is just an average days movement for these whales, so it is not surprising that they are the most well-traveled of the three ecotypes. From the photographic resighting data, we know that the same offshore whales show up off California, Washington State, British Columbia and Alaska, including the waters of the Bering Sea.

It was known from stomach contents, observations and chemical analyses of biopsy samples that offshore whales ate fish, including sharks and halibut, but recently we developed additional insight into their feeding habits. While attempting to photograph a spread out and erratically moving bunch of offshores in Montague Strait, Prince William Sound, we began to notice big flocks of gulls circling well back in the wake of the whales. It seemed that some sort of feed had suddenly shown up for the gulls. What was it? We dropped back to investigate and found chunks of what appeared to be liver (later determined by genetics to be liver from Pacific sleeper sharks) that the gulls were squabbling over. Apparently the offshore whales were killing sleeper sharks and eating their huge oil-rich livers deep below the surface. After the whales had continued on, the buoyant leftover liver bits popped up at the surface to provide an oil-rich bonanza for the gulls. This occurred time and time again as the afternoon wore on, as we traveled in the wake of the whales, grabbing samples before the hungry gulls got to them.

Although our knowledge of killer whales in Alaska has advanced dramatically in recent decades, it is still based on relatively limited research in this vast and remote region. The details of genetic relationships across the regions are just being deciphered; we have only scratched the surface of the killer whale story in western Alaska and we know very little about what occurs in much of the Bering and Chukchi seas. Killer whales may be using far northern waters to a greater degree now that ice cover has been reduced by a warming climate. Certainly there are still many surprises in store for intrepid researchers in these far northern waters.

Another day at the office for Craig Matkin – renowned killer whale researcher and professional model (Bob Pitman using editorial license). Photo by Flip Nicklin

North Atlantic Killer Whales

An Atlantic type 1 killer whale in the North Sea east of the Shetland Islands approaches a fishing boat and shows its worn teeth. Photo by Harriet Bolt ©NAKID Images

by Andy Foote

Distinctive killer whale ecotypes have been found in the North Pacific and Antarctica. Delving deep into museum archives has revealed that two distinctive types also occur in the Northeast Atlantic, as first suggested 150 years ago by Danish taxonomist Daniel Eschricht.

When I found myself working as a naturalist on a whalewatch boat in Northern Norway I had no idea that this was to be the beginning of a long-term project on North Atlantic killer whales. However, a chance encounter in the local marine supplies store with researcher Dr. Tiu Similä, who had conducted two decades of research on North Atlantic killer whales, led to me being invited to help with that year's fieldwork. The special sense of camaraderie and inquisitiveness to learn more about the whales was something that everyone felt working with Tiu. It led me and two fellow research assistants Filipa Samarra and Sanna Kuningas of the Sea Mammal Research Unit to form the North Atlantic Killer Whale ID project (NAKID). Our idea was to work as a multi-disciplinary team and to share research platforms, bring together diverse datasets, link our findings together, and to support one another as Tiu had supported each of us. Soon we had other collaborators onboard including the Marine Research Institute of Iceland and Renaud de Stephanis and his organization CIRCE who have conducted research on the Strait of Gibraltar killer whales for over a decade. However, we were still missing data from around Great Britain.

Finding killer whales in the waters around Britain is no easy matter as they occur at such low density close to shore and the bad weather makes working offshore challenging. However, with help, sightings and photographs from the British public, we have been able to locate and track them in their natural habitat. In the summer, we follow pods of whales as they hug the shoreline hunting for seals. These individuals behave like the mammal-hunting ("transient") killer whales of the North Pacific, hunting in small, silent groups. In the autumn, we join the pelagic fishing vessel, the *Adenia,* during its offshore mackerel-fishing trips. Each time the crew hauls in its catch, groups of killer whales gather around the boat to feed on the injured fish that slip through the nets. At times we have seen more than 100 whales around the boat – what looked like countless fins in every direction. On these trips we use a biopsy dart to collect small pieces of skin from the whales, and extract DNA to test for genetic differences. Photographs provided by the public to the Hebridean Whale and Dolphin Trust identified a third community on the west coast of Scotland that appeared to be isolated from other killer whale groups and had a distinctive pigmentation pattern. They were seen hunting whales, dolphins and porpoises, but would often swim right past seals, seemingly ignoring them.

These observations led us to believe that there might be distinct types of killer whales in the Northeast Atlantic also. However, these field studies provide only a snapshot of the lives of these whales. We wanted to find out if these groups are ecologically divergent over the lifetime of individuals. Luckily we have the resources to answer this question, thanks to generations of diligent curators at our national museums.

Natural history museums are like icebergs – only a fraction is visible from the surface. The majority of the collections are housed out of sight in great warehouses reminiscent of the closing scenes of Raiders of the Lost Ark, but with the rows of arks replaced by hundreds of skeletons of every conceivable type of creature. Now, with the help of new bio-archaeology methods such as ancient DNA and stable isotope analyses, we can unlock exciting new findings from these valuable collections, and learn more about how these different killer whale types lived and evolved.

We started studying these collections in 2006, and by 2009 had sampled close to 100 killer whales from more than a dozen museums. And we started to notice a pattern. Most of the adult-sized specimens had extremely worn teeth, something we had also noted in the field with live killer whales feeding on herring or mackerel. However, a few very large specimens had no tooth wear and also had a lower average tooth count.

At the NERC Life Sciences Mass Spectrometry facility in Scotland, we conducted stable isotope analysis on small amounts of tooth and bone drilled from the museum specimens. This analysis looks at the distribution of isotopes – different types of the same chemical elements – to give an indication of the different types of food the animals were eating. We found that the smaller specimens (type 1, with tooth wear) had quite a varied diet. Some appeared to have foraged mainly on fish, whereas others had a more mammal-based diet. In contrast, the larger specimens (type 2, with no tooth wear) showed almost no variation in isotopic ratios, suggesting their diet was highly specialized. The stomach of one type 2 individual had contained minke whale baleen (the filter plates that sieve small animals from seawater) and field observations are also beginning to suggest this larger type is a specialized cetacean-hunting form.

Genetic work was conducted in Denmark at the Centre for GeoGenetics, University of Copenhagen. This laboratory previously sequenced DNA from mammoth hair and 10,000-year-old sub-fossil human excrement from caves in Oregon, so we were hopeful we could extract and sequence DNA from hundred-year-old killer whale bone and tooth samples. The results showed that the larger whale was genetically different from the more common smaller form – in fact it shared its most common recent ancestor with the Antarctic type A killer whales, which specialize in hunting Antarctic minke whales. The

A comparison of type 1 (top) and type 2 killer whale mandibles in the Natural History Museum of London's collection; characteristic of type 1 killer whales, the teeth in the upper animal were worn to the gum line. Photo by Andy Foote © NAKID Images

A group of type 2 killer whales attack and kill a minke whale off Svalbard in the Northeast Atlantic; notice the characteristic backward-slanting eyepatch of this adult female killer whale. Photo by Dean Gushee

two North Atlantic types could therefore have spent several thousand years apart and had time to adapt to different niches without any interbreeding. These differences may have been exaggerated further if, when the two types met again in the North Atlantic, competition promoted further specialization. Interestingly, when Danish taxonomist Daniel Eschricht inspected some of the same museum specimens in the mid-19th Century, he also suggested that the larger specimens should be classified as a distinct species.

The size differences between type 1 (top) and type 2 killer whales in the North Atlantic are quite apparent when drawn to scale. Illustration by Lucy Molleson

The genetic analysis also showed that the specimens with tooth wear (type 1) belonged to the same lineages as those seen feeding on herring and mackerel in the waters around Scotland, Iceland and Norway. We are not sure, but we suspect the tooth wear could be from sucking up lots of small single prey one at a time, wearing the teeth down over many years. The stable isotope analyses and stomach contents indicated that within each of these lineages, individuals varied in the proportion of mammals and fish they consumed. For example, one adult male had the heads and pelts of 13 harbor seals and several harbor porpoise bones in its stomach; other individuals from the same lineage had just fish bones or seabird feathers in their stomachs. This is consistent with reports from colleagues in Norway who observed two groups of killer whales feeding on both herring and seals.

The story isn't complete yet: we still have more work ahead of us. A key question is whether the two types of North Atlantic killer whales are reproductively isolated: do they (or could they?) still interbreed. This information is crucial in understanding if, for example, they could be different species. So far we've been working with mitochondrial DNA, which is inherited only from the mother; to find out if different maternal lineages are inter-breeding we'll need to use DNA markers inherited from both the mother and the father. Then we'll be able to know if females are breeding with males outside their own lineage or type.

We are also working on even older, sub-fossil specimens dating back more than 10,000 years. This will let us study the ecology of this long-lived species over timescales long enough to show us how these creatures have evolved and adapted to changing environments. The ever-advancing fields of ancient DNA and stable isotope analysis are letting us learn more from our valuable museum collections and providing fresh insights into killer whale evolution. New DNA sequencing technologies are producing exciting studies of both old and new samples. And, in addition to giving us a more objective approach to the classification of types, they're shedding new light on the ecological processes underlying the emergence of these types.

Crozet Killer Whales:

A Remote But Changing Environment

"You go first!" A group of king penguins watch as killer whales practice intentional stranding on the beach of the Baie Américaine, Possession Island. Photo by Christophe Guinet

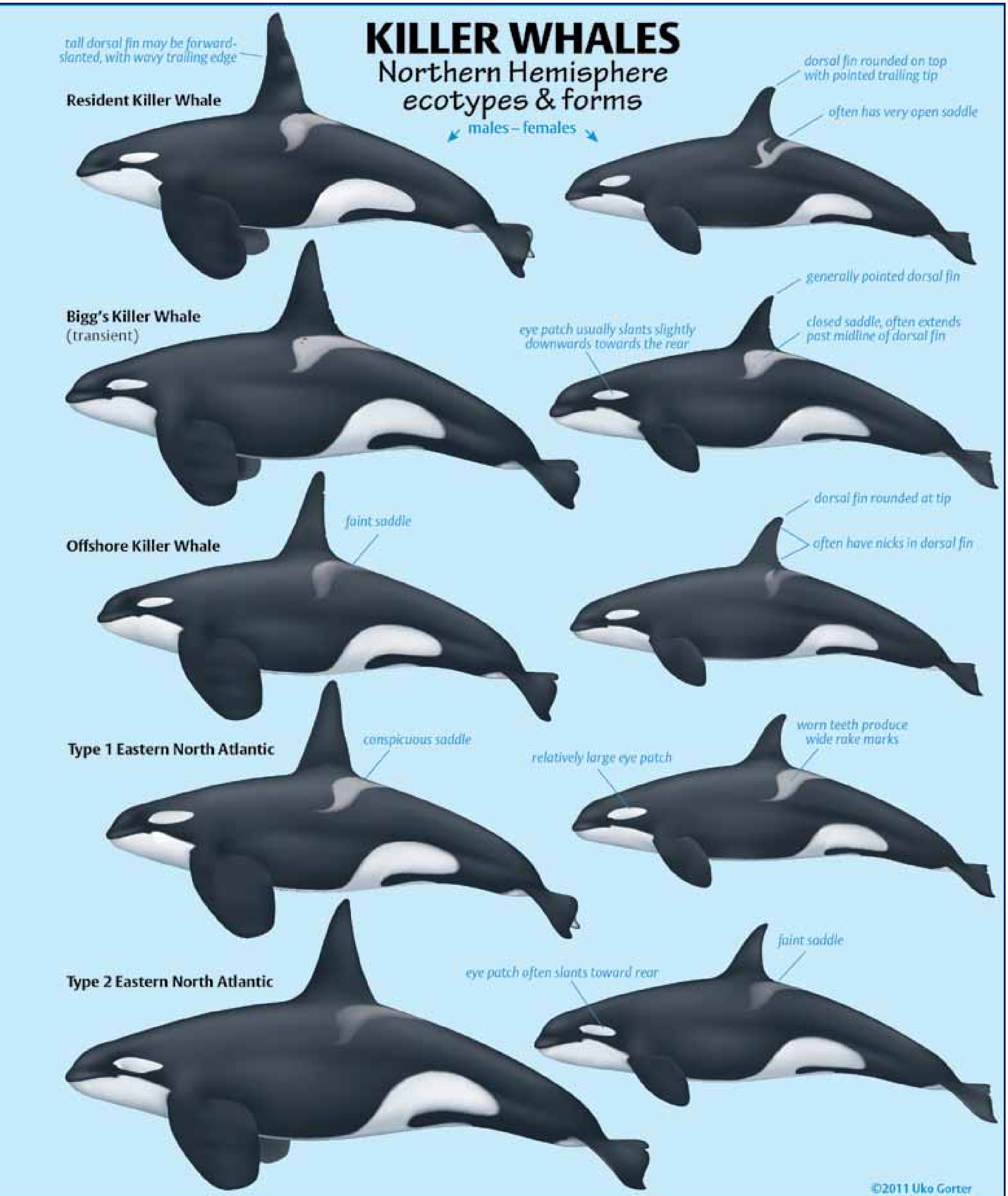
by Christophe Guinet and Paul Tixier

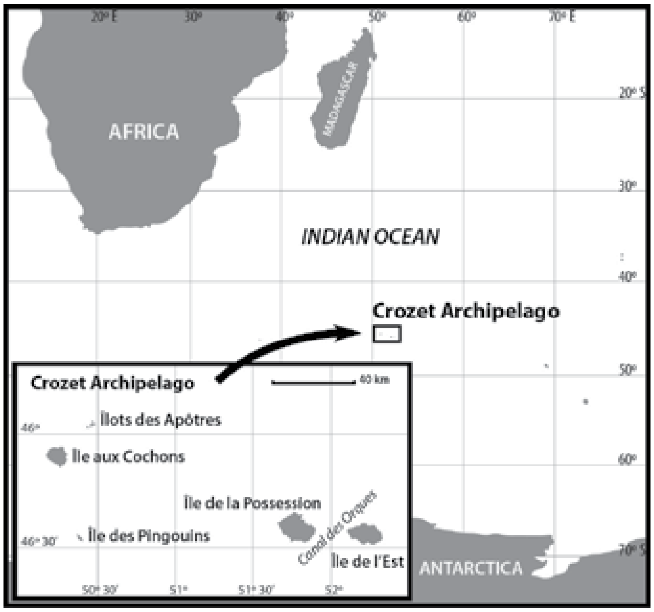
Historically, killer whales were described as capable of feeding on a diverse array of prey, ranging from fishes and squids to pinnipeds, cetaceans and seabirds. However, more detailed studies from different locations have revealed that the majority of the populations exhibit a high level of diet specialization, and that only a few can be described as generalist feeders. For example, in the eastern North Pacific Ocean, three distinct "ecotypes" can be distinguished according to their morphological traits and foraging ecology, and a similar situation occurs in Antarctic waters. In the Indian Ocean, killer whales are widely distributed, including the nearshore waters of Prince Edward, Crozet, Kerguelen, Amsterdam and St. Paul Islands, but there has been no clear understanding of killer whale prey preferences or ecotype distinctions within that ocean.

The Crozet Archipelago (46°25'S, 51°40'E) is one of the few locations in the Southern Hemisphere where killer whale occurrence has long been documented and monitored. The first recorded sighting there occurred in 1825 and first behavioral studies began in the 1970s. Until the late 1990s, killer whales encountered at Crozet were observed mainly from shore. In contrast to most other studies that have found a high level of dietary specialization among individual populations, individual killer whales at Crozet have been observed attacking and feeding on a broad range of prey types including fish, penguins, pinnipeds (seals and fur seals) and cetaceans. More recently, starting in 1996, vessels began fishing for Patagonian toothfish within the Crozet Exclusive Economic Zone, and almost immediately killer whales learned to take fish from the longline hooks as the lines were coming up. The length of these lines varies from 1 to 40 km (0.6 - 24.8 miles), and averaging 8 km/4.9

(continued on page 36)

KILLER WHALES
Southern Hemisphere
ecotypes & forms
males – females
American Cetacean Society
Antarctic Type A Killer Whale
some have slight open saddle
Pack Ice Killer Whale
(large type B)
often has yellow cast due to diatoms
large oval eye patch
dorsal cape; sometimes shows narrow white border
shown without diatoms
Gerlache Killer Whale
(small type B)
often has yellow cast due to diatoms
large oval eye patch, narrower then Pack Ice Killer Whale
dorsal cape; sometimes shows narrow white border
some have slight open saddle
shown without diatoms
Ross Sea Killer Whale
(type C)
often has yellow cast due to diatoms
narrow forward slanted eye patch
dorsal cape
shown without diatoms
Subantarctic Killer Whale
(type D)
dorsal fin swept back
tiny eye patch
bulbous forehead
faint saddle
0
meters
10


KILLER WHALES
Northern Hemisphere
ecotypes & forms
males – females
tall dorsal fin may be forward-slanted, with wavy trailing edge
Resident Killer Whale
dorsal fin rounded on top with pointed trailing tip
often has very open saddle
Bigg's Killer Whale
(transient)
generally pointed dorsal fin
eye patch usually slants slightly downwards towards the rear
closed saddle, often extends past midline of dorsal fin
Offshore Killer Whale
faint saddle
dorsal fin rounded at tip
often have nicks in dorsal fin
Type 1 Eastern North Atlantic
conspicuous saddle
relatively large eye patch
worn teeth produce wide rake marks
Type 2 Eastern North Atlantic
eye patch often slants toward rear
faint saddle
©2011 Uko Gorter



miles. The lines are comprised of a succession of 1 km-long sections, each with 1000 hooks. Longlines are set at depths ranging from 500 to 2000 m (1640 – 6560 feet); this is deeper than killer whales can dive and consequently killer whales strip fish from the line only when the vessels are pulling in their lines. From 1996 to 2000, this fishery was dominated by illegal fishing vessels but navy patrol boats completely stopped illegal fishing by 2003. Currently, there are seven licensed fishing vessels operating within the French subantarctic EEZ, with fishery observers on each of them.

Before the start of the longline fishing, Crozet killer whales were observed and studied only from the shore of the Possession Island (one of the main islands in the archipelago), and this was made possible due to photo-identification techniques developed by Michael Bigg in the early 1970s. Bigg was the first to notice that killer whales each had unique natural markings and that the shape, notches and scarring of dorsal fin, and the shape, coloration and scarring of saddle patch allowed every individual to be identified. The shape of the anterior part of white eye patch, which was also unique to each individual and did not change throughout the whale's life, was also used for identification purposes.

Between 1964 and 1986, numerous photographs of killer whales were taken opportunistically from the shore of the Possession Island by the staff wintering at the Alfred Faure Research Station. Since 1987, a dedicated photo-identification effort was initiated from the shore of Possession Island as part of a long-term program conducted by *Centre d'Etudes Biologiques de Chizé* to monitor marine bird and mammal populations in the French Southern and Antarctic Territories. This work has been supplemented since 1998 by a dedicated photo-identification effort conducted by fishery observers on licensed fishing vessels operating in Crozet waters. Each usable photograph is included in our long-term photo-identification database, along with information on the location of the sighting, total number of individuals photographed, identity code of each individual positively identified in each picture and a "photo quality" grade of the individual in the picture. Currently, our photo-identification database includes over 50,000 killer whale pictures. From this, we have created a catalog of all identified killer whales at Crozet, with individual whales organized into pods (we defined a "pod" as a group of individuals seen together on at least 50% of the sightings).

An analysis of photographic data from 1987 to 1990, before the start of any commercial fishing, revealed a low birth rate and a decrease in the overall number of individuals observed at Possession Island, which suggested that this population was already declining. The data also revealed that killer whales occurred year-round in Crozet waters, but were more abundant from October to December (the elephant seal breeding season) and to a lesser extent during March-April. A shortage of natural prey in the region is a possible cause for this period of slow decline prior to the start of illegal fishing in the area. For unknown reasons, the elephant seal population at Crozet declined by 70% from 1970 to 1990, falling to its lowest documented numbers until 1997. In addition, the whaling industry exploited large whale populations in the southwestern Indian Ocean (among other areas) until 1979 and may have impacted the local killer whales by lowering the abundance of other potentially important prey. At Crozet, for example, killer whales were previously observed hunting right whales and chasing large baleen whales.

Dinner time – A killer whale surfaces next a Patagonian toothfish longliner as the fishermen haul in their lines near Crozet. Photo by Paul Tixier

Further analysis of the photographic data suggested that between 1988-1989 and 1998-2000, when most of the illegal fishing took place, the number of killer whales in the inshore waters of Possession Island declined catastrophically, by about 60%. The estimated survival rate of adults decreased sharply from 94% in 1977 to 90% in 2002. Compared to other well-studied killer whale populations, such as "residents" in the eastern North Pacific, which had survival rates of 96% and 99% in mature males and females, respectively, the apparent survival rate of the Crozet killer whales was strikingly low for both sexes. None of the missing Crozet whales were later observed either from the coast or from fishing vessels. Furthermore, only individuals (not complete pods) were missing. The dispersal of individuals (permanent emigration) was unlikely given the social cohesion of these animals – like killer whales elsewhere, the evidence suggests that Crozet killer whales stay with their pods their entire lives.

Based on this evidence, we suggested that death was the most reasonable explanation for these permanent, abnormally high losses and these probably resulted from active killing of killer whales by Patagonian toothfish poachers during the 1990s. Indeed, witnesses reported that fishermen used explosives and rifles to repel the killer whales coming to their longlines to feed on hooked fish. This increased mortality rate was likely to impact the social organization of Crozet killer whales. For example, the number of lone individuals increased and average pod size decreased suggesting changes in pod composition throughout the study. As killer whales tend to exhibit long-lasting social bonds, modifications in pod structure could therefore indicate a strong disruption induced by the "loss" of a large number of individuals. Furthermore, during that period, the observed birth rate was extremely low with less than one living calf produced per year for 58 killer whales older than one year. This low birth rate coupled with a high mortality of adults would have sent the population into sharp decline.

Since the end of the illegal fishery, the situation appears to have stabilized. Based on photo-identification analysis, the most recent population estimate suggests that a total of about 100 killer whales occur in Crozet waters. And a comparison of the photo-identification work conducted simultaneously from fishing vessels and from shore has brought a new series of findings. First, a second killer whale ecotype was identified in Crozet waters. This ecotype has clearly distinguishable physical features, the most characteristic traits being the extremely small eye patch and a bulbous head more similar to a pilot whale than to other types of killer whales (This killer whale is more correctly termed a distinct "morphotype" because although it is physically distinct from other killer whales, we really don't know anything about its ecology yet). The dorsal fin is also distinctive being narrow with a sharply pointed tip and usually quite backswept. A minimum of 16 individuals have been repeatedly identified in Crozet waters, often interacting with longline fishing vessels. Interestingly, they have never been observed in association with the most common ecotype encountered in Crozet waters and they have never been observed from shore.

The most common ecotype, with a normal-sized eye patch, totals about 85 individuals. Although nearly all of these animals have been seen associated with each other, a comparison of observations collected from land and ship has revealed major behavioral differences among the pods. Indeed, 4 pods totalling 35 individuals were involved in 80% of the fish depredation events, while some pods regularly observed from the shore have never been observed interacting with the fishery, and only a few pods exhibit a moderate levels of interaction with the fishery. This suggests some level of behavioral and possibly dietary specialization within this population. This point will be further investigated in the near future when we conduct stable isotope, fatty acid and genetic analyses using biopsy samples recently collected. The samples are from known individuals of different pods exhibiting different behavior toward the fishery, which will help us address questions of the dietary specialization within this population and to determine how this population is genetically related to others. We are also currently evaluating how these differences in foraging habits affect reproductive success and

This type D killer whale – identified by its distinctive tiny white eye patch and bulbous head - was photographed from a longline fishing vessel near Crozet. Photo by Paul Tixier survivorship in the different pods, and preliminary results suggest that whales that take fish off longlines are, in fact, more successful.

Another interesting observation at Crozet is that killer whale interaction with the fishery started as soon as the fishery was initiated. As killer whales tend to be creatures of habit, this strongly suggests that Patagonian toothfish was probably already part of the natural diet of at least some of the killer whale pods. However, since this fish is a deepwater species, it could be accessible to killer whales only at a limited number of locations such as on sea mounts and within the shallower range of this fish. To address this question we want to deploy satellite tags that will provide information not only on the location of the whale but also on its diving behavior, to look for evidence that it could be a predator of toothfish under natural conditions also. This tag data will also allow us to compare the foraging behavior of killer whales in the presence of fishing vessels versus when they are away from them.

Finally, the photo-identification work conducted from the fishing vessels operating within the French EEZ and Marion Island (South Africa) has revealed for the first time, long distance, longitudinal movements by individual whales ranging nearly 3000 kms (1864 miles), with movements between Marion, Crozet and Kerguelen Archipelago.

Part of our killer whale work conducted in collaboration with the fishery aims at understanding the behavioral processes of depredation and possible mitigation measures to reduce its impact. It was estimated that over 926 tons of Patagonian toothfish were removed from longlines by killer whales and sperm whales at Crozet between 2003 and 2010, representing a financial loss of over $11 million, with killer whales responsible for most of the loss. The work conducted as part of Paul Tixier's Ph.D. has revealed that relatively simple measures were sufficient in significantly reducing killer whale depredation levels. These include such things as reducing longline length, increasing line hauling speed, travelling a minimum of 40 miles from an area where killer whales are present, and fishing during seasons when killer whale pods tend to be busy with other, traditional prey sources, such as during the elephant seal breeding season. But, as a conservation measure, we also want to assess the consequences of this type of foraging on the

The sushi bar is open – a killer whale surfaces next to a longline vessel with a Patagonian toothfish in her mouth that she has just removed from a hook. Photo by Paul Tixier

feeding and reproductive success of killer whale pods that feed this way, according to their level of interaction. The longer term effects of this "supplementary" feeding on killer whale populations will be an important focus of our research for years to come.

Despite the recent, slow increase of prey stocks such as elephant seals as well as the current apparent positive effect of fisheries on growth of certain pods, we still fear that these killer whales may be disappearing along with their unique hunting cultures, such as intentional stranding to capture elephant seal pups and social interactions transmitted to the young individuals by the most skilled females. However, knowledge about this population is still limited to observations from opportunistic and passive platforms; our understanding will benefit from the use of satellite tracking techniques and activity recorders that would yield important information about movements, natural feeding areas and prey types. In addition, collection of DNA samples from killer whales elsewhere in the Indian and Antarctic oceans will increase our understanding of how many types or even species of killer whales there are in the area, and help to define conservation priorities.

It is still too early to know the fate of the Crozet killer whale population, but we do know that the population declines documented over the last few decades would have gone unnoticed (and unexplained) without the continuous and ongoing effort at Crozet, illustrating once again the value of long-term data sets. This work would not have been possible without the dedication of all the observers operating from shore and from the vessels and we thank them for their valuable contributions.

Antarctic Killer Whales:

Top of the Food Chain at the Bottom of the World

My lips are sealed: a pack ice killer whale (Antarctic type B, large form) surfaces off the Western Antarctic Peninsula with a live crabeater seal in its mouth. Photo by Ari Friedlaender

by Robert L. Pitman

Although killer whales *Orcinus orca* are found throughout the world's oceans, they are most abundant in the Southern Ocean (i.e., waters south of 60°S). However, until very recently there has been surprisingly little research or even mention of them there.

The Past

Early Antarctic explorers spent most of their time trudging around on the continent but they also reported some remarkable encounters with killer whales. In 1911, Herbert Ponting, photographer for Robert F. Scott's ill-fated second expedition to Antarctica, was accosted by a pack of killer whales at the ice edge. He just barely managed to escape. The whales apparently were breaking up the ice under his feet as he retreated to safety. Perhaps once killer whales were exposed to photographers they developed a taste for them, because in 1915, another photographer, Frank Hurley, who documented Ernest Shackleton's famous *Endurance* expedition to the Weddell Sea, was also chased by killer whales that broke through the thin ice as they pursued him and his dog team to thicker ice.

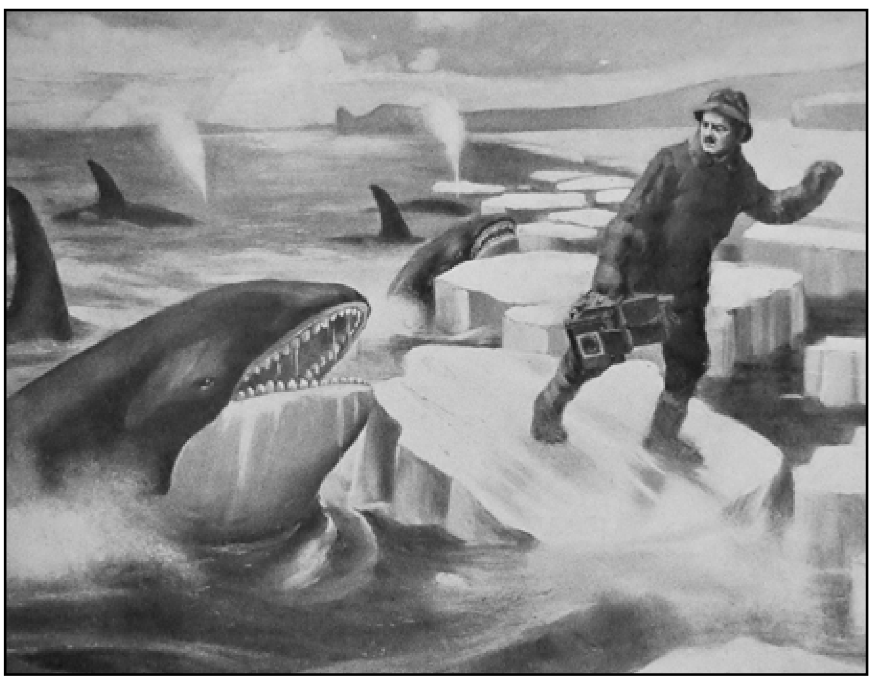
Most of the early accounts of killer whales in Antarctic waters came from whalers during the early 1900s who regularly described marauding bands scavenging on dead baleen whales being towed by whaling vessels. The killer whales usually ripped out only the tongues and lips, apparently their favorite parts, and whalers hated them for it. Armed with rifles, many whaling captains would shoot to kill at every opportunity, and the net effect of whalers both provisioning and persecuting killer whales during nearly a century of intensive whaling in Antarctic waters will probably never be known.

Twentieth century whaling was also the impetus for the first research efforts on whales in Antarctica, but the focus was almost exclusively on large whales; because killer whales were of little commercial value, relatively few were killed and then only opportunistically. As a result, during the 1900s, when nearly two million large whales were removed from the Southern Ocean, only a couple thousand killer whales were commercially landed. Nearly all of the scientific data collected on Antarctic killer whales came from Soviet vessels, which took approximately 26 killer whales per year between 1935 and 1979. In 1979-80, however, during the final season of Soviet whaling in Antarctica, the two Soviet fleets killed a combined total of 916 killer whales. These were the last killer whales ever taken in Antarctica.

In the early 1980s, researchers attached to the two Soviet fleets each, apparently independently, reported a new species of killer whale from Antarctica, based on catches. In 1981, Mikhalev and colleagues described *Orcinus nanus* as a dwarf form – 1-1.5 m shorter than "regular" killer whales – but provided almost no other descriptive details. Furthermore, no voucher specimen (holotype) was collected, which would have allowed other researchers to confirm whether it was a new species. When Berzin and Vladimirov described *O. glacialis* two years later, in 1983, they provided a more detailed description. It was also purported to be a dwarf form: 0.5-1 m shorter than regular killer whales; it ate mainly fish and its skin color had a yellowish cast attributed to a coating of diatoms growing on the body. The authors also included information on bone and body measurements, tooth characteristics, etc., but the holotype that was collected was subsequently lost in a storm that destroyed a laboratory in Vladivostok.

The lack of associated holotype specimens for these descriptions is especially problematic because we now know there are several different types of killer whales in Antarctic waters and trying to match these with either of the Soviet descriptions may not be possible without their original specimens in hand. For example, based on the information they provided, it is not even clear if the descriptions pertain to the same or different "species." Furthermore, currently there are no killer whale specimens from anywhere in Antarctica – there are almost no beaches on the continent for whales to strand on, and too few people to find them if they did.

At about the same time (1979-81), and apparently unaware that the Soviets were describing new species of killer whales, researchers from Hubbs/Sea World Research Institute in San Diego, California, were also reporting different-looking killer whales in Antarctica. From field observations in the fast-ice leads near McMurdo Station in the western Ross Sea, they reported killer whales with a distinct "dorsal cape" (a dark overlay on the back), slanted eye patches and a conspicuous yellow tinge that they also attributed to diatom infestation. Underwater recordings indicated that these whales also had distinct vocalizations, and one was photographed with its head out of the water and a large Antarctic toothfish dangling from its mouth.

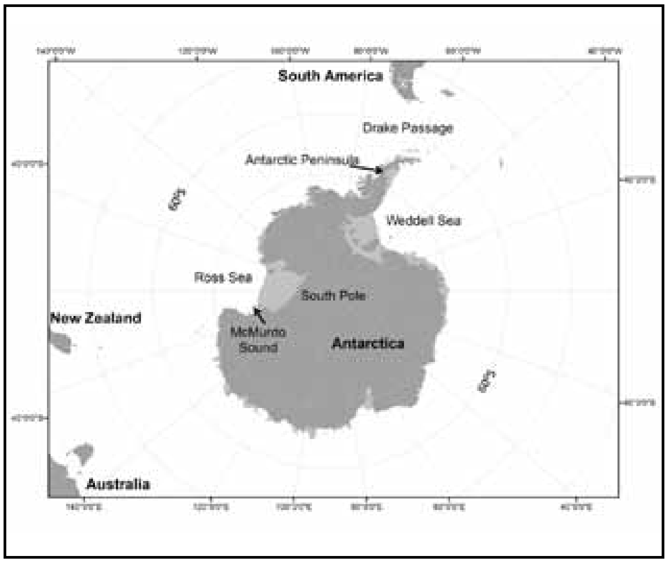


An illustration of Herbert Ponting narrowly escaping attack by killer whales. Taken from Ponting's book "Great White South," an account of experiences with Captain Scott's South Pole Expedition.

Another important event in that pivotal 1979-80 season was the start of a series of cetacean survey cruises in Antarctica initiated under the auspices of the International Whaling Commission (IWC). These eventually surveyed around the entire continent almost three times, over 32 consecutive seasons, aboard Japanese research vessels. Although the cruises focused primarily on assessing the status of Antarctic minke whales, they have also provided the most comprehensive information to date on the distribution and abundance of killer whales in Antarctica during the summer (Dec.- Feb.).

Starting in the 1993-94 season, I participated as a marine mammal observer on six of the IWC cruises. Although the descriptions published by the Soviet researchers did not convince scientists that there were new species of killer whale in the Southern Ocean, those observations, along with those of the Hubbs researchers in McMurdo Sound, suggested that there might be different types of killer whales in Antarctica, including, possibly, a smaller form with a markedly different color patterning.

Motivated by this intriguing possibility, a colleague, Paul Ensor, and I submitted a research proposal and, starting with the 1997-98 cruise, we were granted permission to collect biopsy samples



and photographs of killer whales during those IWC cruises, although always on an opportunistic basis. In addition, we began compiling photographs and sighting records of killer whales from throughout Antarctica. From this, and subsequent field work, we determined that there were in fact *several* types of killer whales in Antarctic waters, forms that were readily distinguishable on the basis of color patterning and with distinct habitat preferences, foraging behaviors, and prey preferences. And although their at-sea ranges often overlapped, they appeared to avoid social interactions and, presumably, interbreeding. This suggested that, at least in some cases, we might be looking at different species of killer whales.

The Present

Currently, we recognize at least five different ecotypes of killer whales in Antarctic and adjacent waters, which we have referred to as types A, B (with a large form and a small form), C and D. Recent genetic evidence published by Phillip Morin and colleagues suggests that at least three of these types (A, large B, and C) could be considered separate species; analyses on the other two types (small B and D) have not yet been completed.

Below I describe the physical characteristics of the five types and discuss what we know about their habits. I also provide some suggestions for common names to replace their former alphameric designations (e.g., “type B”), which have in some cases been in use for almost a decade now – it’s time they had real names.

Type A

This is a “typical” looking killer whale with a familiar black and white color pattern; the eyepatch is of medium size and oriented parallel with the body axis. The maximum body length of this type is unknown, but in the field, adult males in some groups appear to be fairly small (ca. 7 m), while those in other groups are very large (8-9 m). Researchers on Soviet whaling vessels reported individual killer whales in excess of 9 m, but they did not distinguish differences in color patterning, so it is not possible to know for certain which type(s) are represented in their records. In addition, recent analyses have found that type A killer whales have more genetic variability than do the B and C types, so there may be additional types among what we now call type A.

Type A occurs around the entire Antarctic continent where it occurs mostly in open water, seaward of the pack ice. Presumably most of the Soviet catches were of this form because their catcher boats rarely ventured into the pack ice. To date, type A killer whales in Antarctica have been observed feeding only on Antarctic minke whales and once on an elephant seal, but they may also feed the calves of other large whales. It has been assumed that all killer whales, including type A, migrate away from Antarctica during the southern winter and into lower, warmer latitudes, but there have been too few winter cruises in Antarctica to confirm this.

Type B: Pack Ice Killer Whale; Gerlache Killer Whale

Type B killer whales are two-tone gray and white; they have a dark gray dorsal cape and paler gray sides and flanks. The eyepatch is oriented parallel to the body axis and although variable in size it is always much larger than in all other types of killer whales. Some individuals (and often entire groups) are infested to varying degrees with diatoms that turn their white areas yellow and make the gray areas appear brownish. Based on our satellite tracking data it appears that the gray and white individuals have recently returned from a trip to the tropics where the diatoms are shed – a trip to the carwash.

In Antarctic waters, type B killer whales are found around the entire continent where they forage mainly among the pack ice. Type B was originally identified as a prey specialist that fed mainly on ice seals, but working with my colleague, John Durban, in the Antarctic Peninsula area, we have found that there seems to be at least two forms of type B killer whales – a large form we call “pack ice killer whale” that regularly forages in groups that cooperatively create waves to wash seals off ice floes, and a smaller form that forages in more open water, in larger groups and to date has been observed feeding only on penguins. We refer to the smaller form as “Gerlache killer whale” because for many years now large numbers have been reliably found in the Gerlache Strait off the western Antarctic Peninsula.

A type A killer whale chases an Antarctic minke whale off the western Antarctic Peninsula. Although an adult minke can normally outrun a single killer whale, in this case a tag-team of 30 killer whales successfully brought down this minke after a 2.5 hour chase. Photo by Bob Pitman

Pack ice (PI) killer whales are large, robust animals, and based on observations of animals around our launch we would guess they are at least twice the bulk of the Gerlache killer whales. They have a spectacularly coordinated foraging behavior. In open water, groups travel in fairly tight formations, but when they get into an area of pack ice they fan out. Individuals, or cows with calves, begin spy-hopping - lifting their heads above water to have a look around as they swim by individual ice floes. They are looking for seals that often spend their days resting on the ice. When a whale finds a seal, it spy-hops several times around the floe, apparently to make sure it is the right species. They appear to prefer Weddell seals. If it is the right seal, the whale disappears for 20 to 30 seconds, and then begins spy-hopping around the floe again. During the brief disappearance, the whale apparently goes down to call in the troops, because within a minute or two the rest of the group is there spy-hopping around the floe also.

After a minute or two of collective appraisal, the group decides either to move on or to move in and attack. If they decide to attack, the members begin to swim in formation, side-by-side; then they head away from the floe to a distance of usually 5-50 m (15-150 feet). As if on cue, they turn abruptly toward the floe, swimming rapidly with their tails pumping in unison – synchronized swimming. A deep trough forms above their tail stocks and a wave, approximately 1 m (3 feet) high, forms above the flukes. The whales charge the floe and dive under it at the last second. If the floe is small, the wave will break over it and usually washes the seal into the water. If the floe is large (ca. 10 m [30 feet] or more), the whales carry their wave with them under the floe to the opposite side. This often causes the floe to shatter into smaller pieces, after which one or two whales use their heads to push the floe with the seal on it out into open water where they can wave-wash it again.

When the seal goes into the water, the killer whales immediately close in and attempt to take it by its hind flippers to drag it underwater. Although they could at any time easily kill the seal with a single bite or a ramming charge to the mid-section, they

Pack ice killer whales (type B, large form) have located a Weddell seal resting on the ice; on a small floe like this, the seal has little chance of escape. Photo by Bob Pitman

A group of pack ice killer whales (type B, large form) charge an ice floe – the wave being created by their tails will wash the Weddell seal off the ice. Photo by John Durban

choose to wear out the seal and drown it. We think that they want to keep the carcass undamaged so they can take just the preferred bits off of it – much like when they take just the tongues of large whales.

We have seen clear evidence that these killer whales prefer Weddell seals – they sometimes inspect literally dozens of crabeater seals and even leopard seals hauled out on the ice, often within easy reach, but pass them up once they get a good look at them. On the other hand, they attack nearly every Weddell seal that they encounter. It is likely that pack ice killer whales are not always so picky and, like most animals, will pass up less desirable prey only when food is plentiful.

Gerlache killer whales are distinctly different from pack ice killer whales. Overall, they are smaller and slimmer; their eyepatches are large but not quite as big and sometimes they are slightly slanted. They often travel in long, loose groups, as they patrol up and down the straits, preferring more open water – they seem to avoid the pack ice. Also, they regularly feed on penguins and we have seen them take gentoo penguins and chinstraps on numerous occasions. Amazingly, although penguins represent extremely small prey for a killer whale, the whales apparently feed only on the breast muscles and discard the rest of the carcass. This shows once again how selective killer whales can be in their prey choice and how meticulous they can be with their feeding habits. They are so methodical, that we have suggested that at times their prey handling behavior is perhaps best described as "butchering." We have identified hundreds of individual Gerlache killer whales in and around Gerlache Strait during the southern summer and there can't possibly be enough penguins there to feed their legions; we suspect that they may actually feed mainly on fish but to date we have no direct observations.

We are only just starting to understand movements of type B killer whales. We regularly see scars from bites of cookiecutter sharks *Isistius* spp. on the bodies of both pack ice and Gerlache killer whales. The cookiecutter is a small (ca. 0.5 m/1.5 feet) shark that takes only a small bite (the size of an ice-cream scoop) out of much larger "prey," and when the bite heals it leaves a characteristic scar. These are sharks of tropical and warmer subtropical waters, and their scars on Antarctic killer whales is an indication that the whales move to lower latitudes at times. Our preliminary results from satellite tags on both large and small type B whales confirm that both forms probably make regular trips at least to the edge of tropical waters. But when they make those trips they travel fast, move constantly and spend only a few weeks in the tropics before returning to Antarctic waters. We are a long way from understanding the "where, when and why" of Antarctic killer whale movements, how this might vary among the different types and the impact it has on their prey populations.

Type C: Ross Sea Killer Whale

This type also has a two-tone gray and

Seal tsunami – a wave created by a team of pack ice killer whales is about to crash onto this Weddell seal and wash it into the water where the whales will be waiting. Photo by Bob Pitman

white color pattern with a dark gray dorsal cape visible in good light. Like the type B killer whales, some groups or just individuals are also heavily coated with yellowish diatoms at times. The distinctive eyepatch is narrow and tilted forward at a 45° angle. Using aerial photogrammetry (measuring whales from photographs taken from an aircraft), we determined that adult males of this type reach a total length of only 6 m (20 feet) making it the smallest type of killer whale known. In fact, killer whales with males that grow to 8-9 m (26-29 feet), including type A and pack ice killer whales, probably weigh several times

A Gerlache killer whale (type B, small form) chases a gentoo penguin. Normally just the breast muscles of penguins are eaten and the rest of the carcass is discarded. The dorsal cape and large eye patch that distinguish type B killer whales are clearly visible. Photo by Justin Hofman

as much as Ross Sea killer whales and could conceivably prey upon them.
Ross Sea killer whales are known only from east Antarctica where they live deep in the pack ice and patrol leads (cracks) in the fast ice, often miles from open water. They are presumably fish eaters because the only prey identified to date has been large Antarctic toothfish, which can grow to 2 m (6.5 feet) long and weigh over 200 lbs. Not much is known about movements of Ross Sea killer whales, but they have been photographed near New Zealand and Australia, and they also often have scars from cookiecutter shark bites, so they probably are not year-around residents in Antarctic waters.

Type D: Subantarctic Killer Whale.

This is a very distinctive type of killer whale with an extremely small eyepatch and more bulbous head than the other types. It has been sighted only a handful of times and almost nothing is known about it. In 1955, a group of 17 stranded in New Zealand but it was almost another 50 years before that unique eyepatch was recognized again – on living whales near Crozet Island in the southwest Indian Ocean. In the last 10 years type D killer whales have been photographed at sea at least six times, around the globe, in largely subantarctic waters at the northern edge of the Southern Ocean. Therefore, we have suggested the name “subantarctic killer whale” for what we think will likely turn out to be yet another species of killer whale. Nothing is known about its feeding habits except that groups have been photographed attending longline vessels fishing for Patagonian toothfish (a.k.a. Chilean seabass), near the Crozet Islands.

The Future

There is still much to learn about Antarctic killer whales. Based on analysis of killer whale sightings data from 19 separate IWC cruises, Branch and Butterworth estimated in 2001 that the total killer whale population in Antarctic waters during summer was 25,000-27,000 individuals, making it the third most

“Stay in your lanes!” An adult male Ross Sea (type C) killer whale travels along a lead in the thick fast ice of McMurdo Sound, while Adélie penguins watch from the sidelines. Photo by Bob Pitman

abundant cetacean species in Antarctica (after Antarctic minke whale and southern bottlenose whale, respectively), and undoubtedly the largest concentration of killer whales to be found anywhere on earth. But this estimate is itself likely a minimum because a substantial number, and possibly a majority, of killer whales summering in Antarctica regularly occur within the pack ice, a place where the survey vessels generally did not go due to hazardous sailing conditions. Furthermore, this estimate includes all of the different ecotypes lumped together.

Regardless of what the actual total number is, it is clear that killer whales are not only the largest apex predators in the Southern Ocean but they occur in large numbers and are therefore expected to play a major, but as yet largely unknown, role in the Antarctic ecosystem. To date, the geographic scope of our research in Antarctica has been constrained by logistics – nearly all of our research has been restricted to two relatively small but accessible areas: McMurdo Sound and the western Antarctic Peninsula. Our dream scenario would be a research cruise around the entire continent, photographing and tissue sampling animals all along the way, and putting out satellite tags everywhere. This would help us answer some of the most important questions: How many species (or ecotypes, or populations) of killer whales are there in Antarctic waters? When, where and why do they migrate? What do the different types of killer whales feed on? More difficult questions will require longer-term studies: How many individual prey items do the different types of killer whales take during the course of, say, a year? How much impact do they have on their prey populations? How will the different types of killer whales respond to the rapidly changing climate in Antarctica, especially in the Peninsula area where conditions are changing the most rapidly? Are they capable of changing their diet as conditions change?

There are pressing conservation questions also. For example, large scale commercial fishing for Antarctic toothfish has only recently been established in the Ross Sea. This fish is currently the only known prey of type C killer whales and David Ainley and colleagues have already reported what they consider to be a decline in the type C population near McMurdo Sound, which they suggest could be linked to prey reduction by the fishery.

For animals that depend on sea ice, climate change means habitat change, and with it, unforeseen consequences, even for top predators like killer whales. How adaptable the different types, or species, of killer whales are will determine how well they survive the coming changes. What we do know is that as humans continue to alter the planet that we all call home, the perch that killer whales occupy on top of the food pyramid will become increasingly precarious.

Killer Whales of California

MIA: the distinctive LA Pod, once commonly sighted off Southern California, has not been seen since 1997. Photo by Alisa Schulman-Janiger

by Alisa Schulman-Janiger, Nancy Black, and Richard Ternullo

Killer whales occur year-round off California, where nutrient-rich upwellings provide food for a wide diversity of marine life. California appears to mark the southern range of killer whales from as far north as Alaska, as well as the northern range of killer whales from Mexico and the eastern tropical Pacific. Most of the currently recognized types of killer whales in the northeast Pacific have been recorded in Monterey Bay, California. Due to the proximity of its deep, submarine canyon, which regularly attracts numerous killer whales, Monterey Bay is an ideal study location; we have conducted year-around observations there for the past 24 years to learn about their habits. Because so many types of killer whales occur in California waters, understanding their abundance, distribution and natural history is crucial for stock management purposes. Through our California Killer Whale Project (on-going for nearly 30 years), we photo-identify killer whales and keep records of sightings and behaviors; we are also currently in the process of updating our 1997 photo-id catalog – *Killer Whales of California and Western Mexico: A Catalog of Photo-Identified Individuals.*

At least three different ecotypes of killer whales occur in California: 1) “transient” killer whales - mammal hunting, travel in small groups (<10), less vocal, very large body size, pointed dorsal fin often with trailing notches and a large, closed saddle; 2) “resident” killer whales - fish-eating, travel in large groups (20+), highly vocal, large body size, dorsal fin with rounded tip and few notches on trailing edge, and a variably-shaped saddle – often with black intrusions (“open” saddle), and 3) “offshore” killer whales - feed on sharks and fish, travel in very large groups (20-100+), highly vocal, smaller body size, dorsal fin with rounded tip and often with many trailing notches, and usually a closed saddle. These killer whale types differ genetically from each other, with no observations of interbreeding or even social interactions, even when their ranges overlap. They each have distinctive vocalizations, appear physically different to the trained observer, exhibit different social behaviors and hunting tactics, and specialize on different prey. Another, unofficial (no genetic samples), but distinctive type of killer whale that is no longer seen, was named LA Pod. Previously, it was frequently seen off Los Angeles, fed on sharks, sea lions, and possibly fish; traveled in small groups, less vocal, small body size, dorsal fin with rounded tip and often with many trailing notches, and usually a closed saddle.

In Southern California, we have seen other killer whales that have been identified in Mexican waters and offshore waters of the eastern tropical Pacific. These whales have generally darker saddles and often have parasitic barnacles (*Xenobalanus*) attached to the trailing edge of their dorsal fins. We have also documented about 45 killer whales – most sighted just once – that have not yet been linked by association with any of the known types; some even look different. These include a group of at least 20 that attacked a group of sperm whales off Port San Luis, California, in 1997; many of these had very triangular fins with pointed tips and large saddles with dark, circular scars on them from cookiecutter shark bites. These sharks normally occur in deeper offshore waters.

Transient killer whale: This is the most frequently sighted type in California waters, where we have identified over 145 individuals. They range from Southern California to Washington State, although a few have been resighted as far north as British Columbia and Alaska. They are most commonly encountered in Monterey Bay; sightings peak in April and May, when they come to hunt gray whale calves, with another, smaller peak in the fall. They have learned to patrol the edges of the submarine canyon that divides Monterey Bay north and south, where they attempt to intercept gray whale mothers and calves as they cross the canyon. Gray whale mothers are good at protecting their calves in shallow water, but in deep water the advantage goes to the killer whales. Nearly all of the transients known in California have been documented in gray whale attacks in Monterey Bay over the last 20 years, but only eight adult females in various combinations of 2-4 individuals were most active in a majority of those attacks. The attacks usually last from 2-6 hours, while feeding on the carcass can last from 1-2 days. Because most of their prey has acute hearing abilities, transients are generally quiet while foraging in ambush mode, but during and after attacks they become quite vocal. This may attract other killer whales to the prey, sometimes resulting in over 30 killer whales feeding on a single gray whale calf. In addition to gray whales, we have observed transients hunting California sea lions, elephant seals, harbor seals, Dall's porpoise, harbor porpoise, Pacific white-sided dolphins, long-beaked common dolphins, Risso's dolphins, bottlenose dolphins, and minke whales, as well as various seabirds.

Southern resident killer whale: These are normally found off the Pacific Northwest, but K and L pods have recently begun traveling as far south as Monterey Bay. Since they were first sighted there in 2000, they have been observed in the bay nearly every winter. They are now listed as Endangered due to the drastic decline in their preferred food – Chinook salmon – and they may have expanded their range southward to search for this fish, which also faces heavy fishing pressure off California. We report all southern resident sightings to Ken Balcomb (Center for Whale Research, Friday Harbor, Washington), who has studied this population for over 35 years.

Offshore killer whale: These are not as well-known as transients and residents because of their more "offshore" distribution. Some have saddles with cookiecutter shark bite scars. Since 1992, they have been documented over 55 times in California, usually in large groups. Because they frequently travel in sub-groups spread over several miles, it is often difficult to photograph all the whales in a single encounter. We have identified over 200 offshore killer whales in California, although they are seen more regularly off British Columbia. Our collaborative photo-ID work (with NOAA) indicates that offshores have some of the longest movements of any killer whales: two individuals have traveled from Southern California to the Bering Sea in Alaska, a distance of at least 4435 km/2756 miles. We have observed them carrying blue sharks and Chinook salmon in their mouths; elsewhere they have been observed feeding on Pacific sleeper sharks and possibly halibut. They apparently do not feed on mammals; on a few occasions, we have observed them swimming near gray whales, fin whales, and sea lions without showing any predatory behavior toward these species or eliciting any flight response from them.

LA Pod: With over 70 sightings between 1982 and 1997, the 13-15 members of the LA Pod were once the most commonly sighted killer whales off the Los Angeles area. They ranged from at least the Farallon Islands (off San Francisco), south and into the Sea of Cortez, Mexico. They were observed to prey on sharks and sea lions. Their most famous predatory event involved a female, CA2 (~15 feet long), who attacked and killed a great white shark (~10 feet long) off the Farallon Islands in October 1997. Astonishingly, she appeared to immobilize the shark by holding it upside down, causing it to go into a state of tonic immobility. Three members of this pod – including CA2 – were last seen headed south off La Jolla, California, in December 1997, and none has been sighted since. Like other killer whales from Mexico, LA Pod members often had stringy *Xenobalanus* barnacles dangling from the trailing edge of their dorsal fins - so perhaps they have shifted their range south, to Mexican waters.

You can help contribute to the California Killer Whale Project by submitting your photos and sighting information. Your pictures might capture a new transient calf, document a rare visit from residents, help us understand the long-distance travels of the offshores, or answer the tantalizing question of what happened to LA Pod. Please e-mail your photos and sightings to Alisa Schulman-Janiger (janiger@cox.net), Nancy Black (mbaywhale@aol.com), and Richard Ternullo (rternullo@aol.com).

Killer Whale Evolution:

Populations, Ecotypes, Species, Oh My!

Icons of the Pacific Northwest. Killer whales patrol the waters off the Scarlett Point Lighthouse, British Colombia, Canada; how well they can adapt to a rapidly changing marine environment may determine how long they remain in the picture. Photo by L. Barrett-Lennard

by Lance Barrett-Lennard

The famous 19th century whaling Captain Charles Scammon referred to killer whales as "marine beasts that roam over every ocean; entering bays and lagoons where they spread terror and death among mammoth balaenas and the smaller species of dolphins, as well as pursuing the seal and walrus, devouring, in their marauding expeditions up swift rivers, numberless salmon or other large fishes that may come in their way." As with most of his observations, Scammon was essentially correct. Killer whales are found in all of the world's major oceans, do feed on prey ranging from herring to blue whales, and – for good reason – inspire fear in their prey. However, it has become clear in the past couple of decades that the killer whale diet story has a twist that Scammon could not have anticipated. Despite the great variety of prey eaten by the species as a whole, individual killer whales often, perhaps always, focus single-mindedly on a limited set of the prey species available to them. They clearly have very strong ideas about what constitutes food, and may eat only marine mammals, for example, or certain fish species. This predisposition to picky eating is evident in captivity, where killer whales consistently refuse unfamiliar food. Similarly, and despite the fact that his keen eye might have picked out differences in the appearance of killer whales from different areas, Scammon had no way of knowing that killer whales have a xenophobic streak. They go to lengths to avoid other killer whales that aren't part of their population. In the North Pacific (and likely around the world) their populations are small, containing only a few hundred to a few thousand individuals. Finally, we can forgive him – and most biologists for the next hundred years for that matter – for being unaware of the existence of culture in killer whales and many other social animals. Killer whales are quintessentially cultural, passing learned information between generations about foraging areas, hunting methods, dietary preferences, and social behaviors.

While the three strongly-expressed traits described above are undoubtedly products of evolution, it is their potential impact on evolution in the future that I find most interesting. Evolutionary change occurs in fits and starts, and so-called "adaptive radiations" that rapidly generate new species often follow key evolutionary innovations. Classic examples would be the radiation of birds following the evolution of flight, or of mammals after the evolution of placenta to nourish offspring prior to birth. It is at least possible, therefore, that the combination of diet selectivity, xenophobia (perhaps better described as social exclusivity) and a strong dependence on culture have set the stage for an adaptive radiation of killer whales – a possibility I discuss later in this article.

Slammin' salmon - a southern resident killer whale with the catch of the day: a wild-caught chinook salmon. Photo by Brian Gisborne

Killer Whale Populations and Ecotypes

It was the late Dr. Michael Bigg who first recognized that within his study area – the coastal northeast Pacific – two killer whales ecotypes (ecologically distinct populations) were present, one of which preyed exclusively on fish and the other on marine mammals. Because the movements of the fish-eating group were more short-range and predictable in the summer field season than those of the mammal-eaters, he referred to the two groups as residents and transients, respectively. Based in part on their smaller group sizes, Bigg originally suspected that transients might be social outcasts from resident killer whale pods, but by the late 1970s he realized that they were distinct, independent groups. Furthermore, he noted that there were two geographically adjacent "communities" of residents off the Washington and British Columbia coasts, which he referred to as southern and northern residents. Shortly before Bigg's death in 1990, a fourth discrete set of killer whales was discovered off the British Columbia coast. Referred to as offshores, members of this group appeared to spend much of their time further away from the mainland coast than the transients or either of the resident populations. It is now known that both resident communities have a strong preference for Chinook (or king) salmon, the largest – but least abundant – of the five salmon species found in the area. The primary prey of transient killer whales are harbor seals, Dall's and harbor porpoises, Steller and California sea lions, and gray and minke whales. The diet of offshore killer whales is less well understood, but is known to include sleeper sharks and halibut.

In the decades following Bigg's discovery of resident and transient killer whales in British Columbia, additional populations of fish-eating and mammal-eating killer whales have been found off Alaska and the Russian Far East near Kamchatka. The offshore population is now known to roam as far north as the eastern Aleutian Islands and as far south as Southern California. Across the entire area, populations belonging to different ecotypes overlap extensively. In contrast, populations within an ecotype overlap minimally, likely because they would compete for prey. In the absence of physical separation, the separation of populations must be maintained by social mechanisms, and indeed, researchers have long noted that members of different populations consistently avoid close contact.

The repeating pattern of overlapping ranges of fish-eating and mammal-eating killer whales along the west coast of North America and the Russian Far East raised the possibility that the evolution of the two ecotypes had occurred multiple times, but recent genetic research strongly favors a single separation. In other words, the

A landmark study by John Ford in the 1980s revealed that each resident killer whale pod has a unique dialect. Photo by Nancy Black

split between these two forms occurred just once: all the fish-eating populations in the North Pacific share a more recent ancestor with each other than with the mammal-eaters, and vice versa. However, this pattern does not hold around the world. Some mammal-eating killer whales in the Southern Hemisphere are more closely related to residents than transients. For this reason, we do not refer to all fish-eating killer whales around the world as residents or to all mammal-eaters as transients. The names refer to assemblages of related populations, not to the ecotypes they belong to. The origin of the offshores is somewhat enigmatic...one explanation of the genetic findings is that offshores split from residents well after the resident-transient separation, but females occasionally mated with transient males. In any case, the complete or near-complete reproductive isolation of transients, residents and offshores helps explain the existence of subtle but consistent differences in their fin shapes and pigmentation patterns first observed more than two decades ago.

Research by Bob Pitman and colleagues in Antarctica has revealed an even more complex set of killer whale ecotypes than those of the North Pacific, as described in another article in this issue. These groups differ from each other more in appearance than do residents, transients and offshores. It is not clear at this point whether any or all of the Southern Ocean ecotypes contains more than a single population, but in any case the general pattern of overlapping or adjacent populations that maintain their separation by behavioral means alone and have different hunting behaviors and dietary preferences is similar to that found in the North Pacific. Recent research by Andrew Foote and colleagues in the North Atlantic provides preliminary evidence of at least two discrete populations belonging to different ecotypes there as well.

Sound Evidence of Culture

Killer whales, like other toothed cetaceans, use sound for communication, navigation, and locating prey. A landmark study by John Ford in the 1980s revealed that each resident killer whale pod has a unique dialect (repertoire of stereotyped calls), so that pods of northern residents can be unambiguously divided into three “clans” based on dialect similarity, and that pods of the smaller southern resident community belong to a single clan. Ford also showed that transient killer whales use stereotyped calls as well, albeit much more sparingly than residents, but they do not appear to be divided into clans. I studied the use of killer whale echolocation in the early 1990s and found that transients use echolocation much less frequently and conspicuously than residents, and some years later Volker Deecke showed that transient killer whales are most vocally active immediately after a successful attack and rarely call while hunting. Both patterns likely reflect the fact that marine mammals have more sensitive hearing than fish and are better able to successfully avoid predators when they detect them. How transients navigate and locate prey while using little if any echolocation is still an open question, but the most likely explanation is that they rely to a great extent on passive listening---using ambient soundscapes for navigation and eavesdropping on the vocalizations and swimming and surfacing sounds of their prey. Studies of the acoustic behavior of offshores are at an early stage, but they are known to call and echolocate frequently, leading researchers to believe that their diet includes few if any marine mammals.

The observation that resident pods have distinct dialects raises the question of whether call repertoires are learned through some cultural process, or inherited. Two lines of evidence indicate that they are learned. First, in captive settings young killer whales learn and use the calls of unrelated older tank mates. Second, research on mating patterns in northern residents and southern Alaskan residents has shown that in those populations almost all mating occurs outside the pod and most occurs outside the clan. Both males and females spend their lives with their mother and use her calls rather than those of their absent father. A genetic mechanism that would cause calls to be inherited from one parent and not the other is unlikely. It is more difficult to determine whether the differences in echolocation by residents and transients reflect culture or inheritance, but since captive killer whales can learn to modify their echolocation use in captivity, a role for culture is likely.

In addition to vocalizing, a number of other important behaviors are transmitted culturally. For example, in the Crozet Islands adults teach stranding behavior to calves by gently but repeatedly pushing them onto steeply-sloping beaches where than can easily wriggle back into the water. The risks inherent to stranding are greatly reduced by learning, and it is an effective strategy for attacking fur seal and elephant seal pups. Rubbing on traditional pebble beaches is a culturally-transmitted social behavior commonly practiced by northern resident killer whales. Transient killer whales at Unimak Island, Alaska, leave gray whale carcasses in shallow water and return to feed on them over a number of days – a caching behavior not known in other groups of mammal-eating killer whales and presumed to be culturally transmitted.

The fact that killer whales are capable of learning and culturally transmitting complex behaviors, as illustrated by the examples above, does not mean that they are particularly adept at coming up with novel behaviors on their own. Indeed, they strike many researchers, particularly those who have studied them in captivity, as conservative animals - capable of learning practically anything by example, but not prone to experimenting and innovating. For example, captive killer whales are far less likely to pass through a gate or investigate and play with novel objects in their pools than other members of the dolphin family - unless a poolmate or human trainer does so first. Depredation (taking fish off fishing gear) provides another example. In the wild, killer whales and fisheries often coexist for years

Killer whale families are typically more stable than those of humans, and with a bit of luck this female transient killer whale (foreground) and her calf will spend at least the next 50 years together. Photo by Bob Pitman without interacting. However, once a few individuals learn to raid fishing gear the behavior can spread through the population very quickly.

Evolutionary explanations for traits such as behavioral conservatism are easy to propose and difficult to test. Nevertheless, a plausible explanation is that there has been stronger selection for social than for experiential learning because the former is inherently safer. Animals that are long-lived and slow-reproducing avoid risk because the evolutionary costs (increased probability of death before successful reproduction) are high compared to the benefits (a few more surviving progeny). Furthermore, individuals living in stable social groups like killer whales have reliable models to learn from - every mother with surviving offspring and every sexually-active adult male is living proof of the virtue of his or her behaviors.

Speciation in Killer Whales

As described earlier, killer whales live in a bewildering array of populations clustered within an extraordinary array of ecotypes. In this sense, they are quite unlike any other well-studied animal with the possible exception of humans. Before considering whether there are multiple species of killer whales - or indeed whether it is worth going through the exercise of defining species boundaries in such a taxonomically unruly throng - it is worth trying to understand how such complexity arose. Here, the first defining killer whale trait listed at the beginning of this article - social exclusivity - is of paramount importance. Before developing that theme further, however, a brief primer on speciation.

Evolutionary biologists have recognized for many years that gene flow within a population is the principle impediment to speciation. Populations often experience so-called disruptive natural selection, where individuals with traits that are separated on a continuum (for example, large and small size) are more successful than those in the middle. However, disruptive

Seal Team – transient killer whales skulking along a shoreline in the eastern Aleutian Islands looking for mammalian prey; individuals in this group may have been hunting in these waters together for decades. Photo by L. Barrett-Lennard selection can't cause speciation if positively-selected individuals, in this example, large and small members of the population, keep breeding with each other. The most straightforward way for speciation to occur is for a barrier to develop that physically divides a population - for example continental drift, or climate change that renders a mountain range impassable. This is called "allopatric speciation," and is thought to explain most existing biodiversity. Allopatric speciation does not require disruptive selection because "genetic drift" causes separated populations to diverge genetically over time. There are a variety of ways by which speciation can occur "sympatrically," in the absence of physical separation, but they all require some mechanism to prevent or greatly restrict gene flow between groups.

The marine environment has few barriers for a species capable of long-distance travel and tolerant of wide ranges of temperature, so killer whales, and many other cetaceans for that matter, are unlikely candidates for allopatric speciation. This is where social exclusivity comes in. Killer whales live in stable social groups with limited or no dispersal of members. They stay with their mothers and siblings their entire lives. In resident populations, and perhaps most others, these groups are called matrilines - a matriarch and her descendents. Social groups in a common area encounter others frequently, providing opportunities for cooperative foraging, mating, and shared territorial defence. All of these factors promote social cohesion, shared cultural traditions and the development of, in a literal sense, community. As previously mentioned, members of a community actively avoid close physical contact with members of other communities. The reason for this apparent xenophobia is unknown, but one could speculate that inter-community contact has few benefits and many risks, such as competition for food, disease transmission, and aggression arising from the lack of shared social traditions. In any case, by presenting a behavioral barrier to social contact, and hence mating, social exclusion restricts gene flow and allows populations to diverge genetically.

I've argued that social exclusivity predisposes killer whales to form diverse, genetically isolated populations – incipient species, effectively. There seems to be lots of potential for further evolutionary divergence, but whether it will in fact occur depends on whether it exceeds the population extinction rate. In other words, we could be lucky enough to be witnessing the early stages of an adaptive radiation of killer whales whereby a variety of new species will exploit diverse ecological niches – or we could be looking at an ongoing process by which new ecotypes form and periodically wink out. Suffice to say that all the ingredients for an adaptive radiation, no matter how ephemeral, are present. The traits of diet selectivity and culture go hand in hand with social exclusivity to help discrete killer whale populations form and diverge ecologically and genetically. Diet selectivity makes it possible for populations to overlap without competing. It must also inevitably drive the evolution of adaptive differences over time. For example, natural selection likely favors agility in fish-hunting killer whales and robustness in those hunting mammals – transients have heavier jaw musculature than fish-eating residents. Culture is a likely an important driver of adaptive evolutionary diversification as well, not only because it defines communities and helps maintain their reproductive isolation, but because it helps them maintain a body of information for consistently finding large prey or large patches of prey in a background of long term and short term environmental variability. Large or concentrated prey are essential if killer whale groups are to stay together, no matter which ecotype they belong to, and group cohesion is, as I've argued, necessary for community maintenance.

Phillip Morin and colleagues recently proposed that three new killer whale species and a number of subspecies be designated. Their proposal was based on the identification of well-defined clades (branches on an evolutionary tree) in maternally-inherited mitochondrial DNA of a large number of killer whales sampled around the world. While the findings are extremely interesting, I'm withholding opinion on the proposal pending further studies focusing on association patterns, ecological specialization and nuclear DNA. If I'm correct and killer whales are in the relatively early stages of an adaptive radiation, the populations we see at present represent a continuum of continually diversifying forms. In this type of evolutionarily-dynamic situation any of these forms could well develop into a fully-independent species. Until we better understand the processes generating this diversity (the brushstrokes in the picture I've presented here being very broad), I believe the best strategy is to recognize *Orcinus orca* as a species complex and to resist the temptation to revise its taxonomy formally. Whether or not this advice prevails, it's clear that the astounding worldwide diversity of killer whale types will generate fodder for scientific enquiry for years to come. It's going to be a fascinating ride, and I'm looking forward to it!

Predators, Prey, and Play:

Killer Whales and Other Marine Mammals

Killer whale hunting at a sea lion haulout. Despite hundreds of sea lions at this site, the whales feed almost exclusively on harbor seals when hunting there. Photo by Robin Baird

by Robin W. Baird

While working on his Ph.D. on harbor seals in the late 1980s, Peter Watts spent a lot of time watching seals at several harbor seal haulouts in Puget Sound, in the Strait of Georgia, and in Howe Sound in British Columbia. Over hundreds of hours hanging out with the "prey," Peter had never seen killer whales foraging at any of these haulout sites. Yet where I was working around the southern tip of Vancouver Island, between the Strait of Georgia and Puget Sound, a typical day following "transient" killer whales usually involved watching them catch and consume at least a couple of harbor seals. One day in 1992 I watched two whales kill nine harbor seals in three and a half hours! I was following the predator. Peter was watching the prey. If you happen to be prey, your individual chances of getting eaten are rather small – it only happens once in your life, at most. But if you are a predator you are probably eating prey on a regular basis. If you are a killer whale and harbor seals make up a large proportion of your diet, typically this means catching a seal at least once a day.

Most killer whales hunting harbor seals travel in small groups and share their prey, so actually chasing, catching, and consuming seals probably happens several times a day. If you spend your time watching harbor seals at a haulout, you are likely to conclude that predation isn't important, whereas when you follow the harbor seal predator, in this case "transient" killer whales around southern Vancouver Island, it quickly becomes clear that predation on the seals is a regular event, and can certainly strongly influence seal behavior, as well as potentially play an important role in seal population dynamics. Some back-of-the-envelope calculations in 1989, after three years of watching killer whales hunt seals around Victoria, seemed to indicate that not only were killer whales probably the most important harbor seal predator, but they could be responsible for a large proportion of the natural mortality of harbor seals in the area. Despite this, harbor seal numbers were increasing at the time, and had been for a long time since the bounty on seals ended in the area in the 1960s.

Whether killer whales might substantially influence prey numbers will of course depend on the relative densities of the predator and prey, and on how specialized individual killer whales are within a particular population– whether they are mammal-specialists or fish-specialists as are those found in high latitude populations, or are more generalists like those found in some lower productivity, tropical areas. Much of my work for the last 12 years has focused on studies of odontocetes in the tropical waters around the main Hawaiian Islands. In 2003 while undertaking a survey off the west side of the island of Hawai‘i we spotted a group of small black whales scattering in several directions at high speed. We were following the small black whales, later confirmed to be melon-headed whales, to try to get photos and figure out what they were, when one of the crew mentioned possibly seeing a killer whale when the panicked little whales were first spotted – certainly that would be a good reason to flee. This was our fourth year of field work in Hawai‘i, and only our first killer whale sighting. We collected a biopsy sample and photographed the four killer whales; analysis of the biopsy sample later revealed a unique mitochondrial haplotype, most closely related to mammal-eating killer whales sampled off Alaska.

Although we did not see them catch any melon-headed whales, the reaction of the melon-headed whales certainly implied they viewed the killer whales as a threat. Were these “transient” killer whales from the west coast of North America on a far-offshore hunting trip? Not likely – in fact the whales looked different than coastal killer whales, with narrow and faint saddle patches, and regular scars from cookiecutter sharks, and were likely part of an open-ocean population inhabiting the central tropical Pacific. Seven years of additional survey effort in Hawai‘i and our tracklines add up to the equivalent of boating around the circumference of the world more than one and a half times, and we have yet to see another killer whale there. We do hear of one or two sightings a year around the main Hawaiian Islands, and killer whales in the area have been recorded attacking a humpback whale, eating a shark and an octopus, and with squid beaks in their stomachs – they appear to be generalists, rather than specialists, not surprising given the overall low productivity of the central tropical Pacific. Given the paucity of sightings, and the apparent breadth of their diet in Hawai‘i, killer whales probably have little impact on populations of different species of marine mammals in the area, despite the reactions of the melon-headed whales.

There is no doubt that a risk of getting eaten by killer whales influences the behavior and biology of their prey, whether it is hauling out behavior of seals or sea lions, vocalization patterns of porpoises (they vocalize at such high frequencies that killer whales cannot hear them), and potentially even the seasonal migratory patterns of large baleen whales. It has recently been suggested that the cryptic behavior of beaked whales, only vocalizing at depth and avoiding near-surface waters particularly during the day when visually-oriented predators like killer whales are more likely to be hunting, may be due to avoiding predators like killer whales. The schooling behavior of many species of dolphins may reduce the likelihood that any one individual in the group is taken by a hunting killer whale.
It may seem obvious to state that killer whales aren’t baleen whales, but they do share some tendencies. Some baleen whales are well-known for their seasonal variations in behavior, typically spending the spring through fall feeding intensively and building up blubber stores for a winter spent in more tropical breeding areas, where feeding is rare. Toothed whales feed year-round, but at least some killer whale populations experience seasonal variability in food intake, albeit to a lesser extent than some baleen whales. In the Salish Sea, harbor seals typically give birth in mid-summer. Pups remain hauled out or close to their mother for the first six weeks of their life. After that they are on their own, naïve, and trying to learn how to survive. In late summer and early fall (August and September) the number of

No rush: a live harbor seal in the mouth of a mammal-eating killer whale, being carried awhile before it is killed. Photo by Candice Emmons/NOAA Fisheries

A badly battered minke whale seeks a moment of respite from its tormentors, but the transient killer whales are going to win this contest. Photo by Dave Ellifrit

naïve seals in the water increases dramatically, providing easy prey to mammal-eating killer whales.

From following groups of killer whales and examining food intake rates, I determined that during this period the whales consume about twice what they do during the rest of the year and much more than they need to eat – killer whales are like baleen whales, stocking up on food when it is abundant, allowing them to get through leaner times. The same is probably true for the fish-eating "resident" killer whales that spend much of their summer and fall in inshore waters, gorging on salmon that are concentrating in areas off the mouths of rivers that they will soon move into to breed. Such seasonal variation in food intake makes it difficult to extrapolate from observations in one area or at one time of the year, to determine what role killer whales may play in regulating the numbers of their prey.

What impacts killer whales have on the numbers of their prey and the potential for driving large scale changes in prey abundance is somewhat controversial. In 1998 Jim Estes and his colleagues suggested that killer whales were the likely cause of a large-scale decline in numbers of sea otters in the Aleutian Islands. Sea otters had never been considered an important part of the diet of mammal-eating killer whales. Otters rely on their dense coat, rather than a thick blubber layer, to keep warm, and thus are less likely to be chosen as prey, if the killer whale has a choice. But in the 1990s, there were increased observations of killer whales attacking or otherwise interacting with sea otters in the Aleutians, although the number of attacks observed was small and the outcomes of the attacks were not always confirmed – sometimes the otters got away or were possibly just being harassed. In one area, a large lagoon that was inaccessible to killer whales, otter numbers were stable, whereas in a nearby area exposed to potential predators otter numbers were declining.

The story was convincing and widely accepted, but a recent re-assessment of the evidence by Katie Kuker and Lance Barrett-Lennard, including information available in the 10+ years since the original publication, suggests that the jury is still out – increases in shark populations in the same time period, high levels of persistent organic pollutants such as PCBs, and potential disease outbreaks, could all have played a role in the decline of sea otters in the Aleutians. Even the observations of attacks are subject to some uncertainty – fish-eating killer whales do occasionally play with other marine mammals in a way that could easily be interpreted as a predatory attack. In the San Juan Islands, observations of fish-eating killer whales "playing" with porpoises were uncommon throughout the 1980s and 1990s, while in 2005 they increased in frequency, with eight such events observed. The whales' motives did not appear to be food consumption. There was no evidence any of the porpoises were consumed, but some of the porpoises were killed, and the fish-eating southern residents have been observed playing with and sometimes killing porpoises much more frequently in the last seven years than they had in the first 30 years of study of this population. Whatever the motivation, it doesn't really matter to the porpoise, or potentially to porpoise population dynamics, if they are killed by a killer whale.

The oceanic ecosystems in which killer whales live today have changed dramatically in the last few hundred years. Populations of many species of whales and dolphins were greatly reduced by large-scale commercial whaling or by bycatch in commercial fisheries, many pinniped populations were reduced due to hunting or culling, or more recently due to collapses in fish populations caused by over-fishing, and numerous fish populations have been harvested to the point where the populations have collapsed, and few have recovered. Such changes in prey populations not only may have influenced what killer whales feed on today but also what role killer whales have played in food web dynamics.

Teamwork: a pod of transient killer whales work cooperatively to separate a gray whale calf from its mother (left) in Monterey Bay, California. Photo by Alisa Schulman-Janiger

In 2003 Alan Springer, Jim Estes, and their colleagues, championed the view that reduction of large whale populations in the North Pacific by commercial whaling resulted in a greatly depleted prey base for mammal-eating killer whales, resulting in killer whales switching their diet to smaller prey such as pinnipeds and sea otters, eventually resulting in the sequential collapse of many of those populations in the area. Their hypothesis has received plenty of attention, a fair share of criticism, and a number of rebuttals – a detailed review of the arguments on both sides would fill this issue of *Whalewatcher*. Rather than summarize these, I offer my own "two-cents," in particular on the issue of whether large whales were ever an important part of the diet of mammal-eating killer whales in coastal areas where large whale populations overlap with pinniped and sea otter populations.

Given a choice, whether a killer whale will decide to attack a large whale, a seal or sea lion, or a sea otter, will depend on how profitable and how risky the different choices will be. Adult male sea lions or large whales can both fight back, and thus there is some risk to attacking them. Having a risk of getting killed or injured over a meal makes it a poor choice, unless it is the best choice available. What that means is such choices will depend not on the availability of whales or sea lions to hunt, but whether there are other, less risky, or more profitable, prey around. If you are a mammal-eating killer whale, the ideal prey is not only going to be high in energy, but be easy to kill, with little or no risk of getting injured when doing so. Elephant seals are probably one of the most preferred prey, easy to kill, lots of energy, and not particularly dangerous when in the water. Harbor seals and harbor porpoise are probably high on the list, but most of the large baleen whales, and sperm whales, are likely near the bottom, at least as adults. Sea lions and sea otters are probably somewhere in the middle, and in the case of sea lions the choice will depend in part on the age and sex of the sea lion, how close to shore (i.e., a refuge) it is, and how big is the group of killer whales that find it. In a large group, the whales can cooperate in the attack, reduce the risk of injury, and the likelihood of the sea lion escaping. In terms of the sequential megafaunal collapse hypothesis, this suggests that, at least in coastal areas where the whales likely had, or have, a choice, large whales were probably not particularly important in the diet of mammal-eating killer whales. Do the mammal-eating killer whales spend most of their time on the continental shelf where they are most likely to overlap both with a number of species of pinnipeds and large whale species? Evidence from mammal-eating killer whales satellite-tagged in an area southeast of where the population declines have occurred, off the Washington coast, suggest mammal-eating killer whales in that area do spend most of their time on the shelf, but some animals tagged in western and central Alaska by John Durban and colleagues have ranged further offshore. Unfortunately, assessing where the killer whales that live around the Aleutians spent their time prior to and immediately after the heavy exploitation of large whales will never be possible.

Killer whales are at the top of the food web, but their position there is precarious. As top predators, killer whales accumulate persistent organic pollutants such as PCBs and flame retardants more so than predators further down the food web. Since they are long-lived, mature slowly, and reproduce so infrequently, such toxins may build up to levels that may be affecting their reproduction or their susceptibility to disease. Such impacts are insidious, and by the time they are obvious to us it will be too late to do anything about it. If we want killer whales to remain a functioning part of the ecosystems in which they live, some action to deal with these pollutants is needed on both a national and international scale.

Killer Whale Conservation:

The Perils of Life at the Top of the Food Chain

Trophic cascade – killer whales charge by a fishing boat at Crozet looking to strip toothfish off longlines while black-browed albatrosses and white-chinned petrels follow, looking for scraps from the whales. Photo by Paul Tixier

by Lance Barrett-Lennard and Kathy Heise

In the first century AD, the Roman scholar Pliny the Elder described the killer whale as an "enormous mass of flesh armed with savage teeth." Killer whales have long been known to hunt in packs and to attack and kill prey much larger than themselves. For millennia, seafarers the world over accorded them the same kind of fear – and often loathing – that land dwellers did the wolf. It would no doubt come as a surprise, then, for those mariners of the past to learn that killer whales are far more vulnerable to humans than were the dolphins that played under their bows.

Various features of killer whale life history and ecology account for this vulnerability. First, killer whales are not abundant, and rare species are generally at greater risk of extinction than common ones. The energy available to sustain life diminishes with each step up a food chain, and ecosystems simply cannot support many top predators. Second, they have a very low reproductive rate: female killer whales don't reach sexual maturity until their teens and then produce only one calf at a time. Surviving siblings are usually separated by four years or more. This low reproductive rate means that killer whale populations recover very slowly – if at all – from spikes in mortality. Third, killer whales are highly dependent on healthy ecosystems. They depend not only on their prey but indirectly on their prey's prey as well, and so on down the line. Fourth, killer whales are long-lived, perhaps 60 and 80 years for males and females, respectively. Coupled with their position at the top of the food chain, this results in staggeringly high accumulations of contaminants such as heavy metals and PCBs. Fifth, the highly social nature of killer whales makes populations vulnerable to catastrophic events. A single oil spill occurring near a seasonal "superpod" aggregation could decimate an entire community of killer whales. Sixth, the survival of calves and juveniles is highly dependent on care by mothers and other relatives. This means that the premature death of an adult female killer whale can lead to the deaths of other members of her "matriline" (her siblings and offspring). The rest of this paper should be read in the light of this laundry list of inherent vulnerabilities of killer whales to natural events and human-caused activities such as environmental change and fishing and whaling. Perhaps the most remarkable thing about this charismatic species is that it has persisted as long as it has.

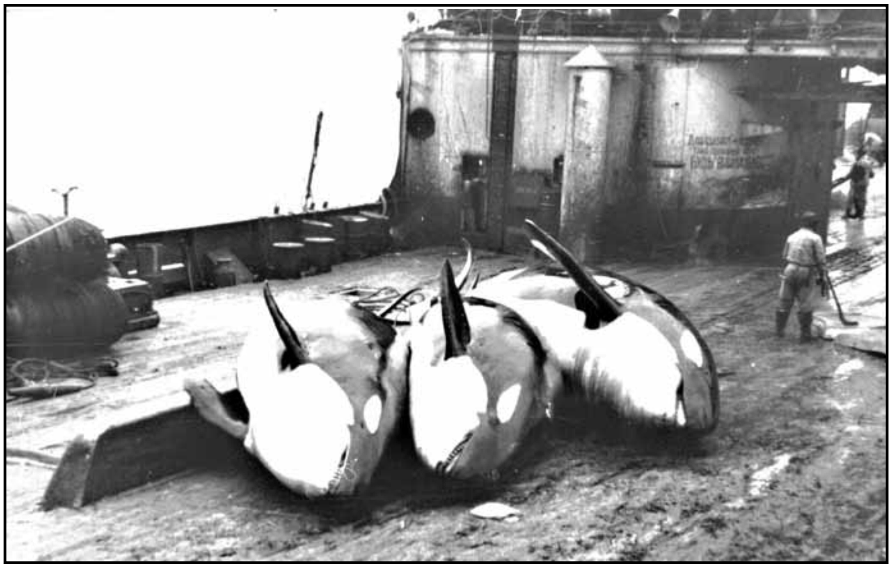
The problem of conserving killer whales is greatly compounded by the fact that we do not know how many species there are. In the northeast Pacific, for example, there are at least seven discrete populations ranging in size from less than a hundred to a few thousand individuals, each of which belongs to one of three ecologically-distinct groups ("ecotypes"). All of these populations are genetically distinct, despite having overlapping ranges; all appear to have unique cultural traditions, and some are noticeably different in appearance. As discussed in the evolution article in this issue, each ecotype in the northeast Pacific belongs to a different "clade" (genetic grouping) suggesting to some researchers that three species of killer whales should be recognized in the northeast Pacific. Whether or not those species come to be formally accepted, it is clear that what we call *Orcinus orca* is a complex of populations sufficiently diverged to be considered, at the very least, incipient species. Both Canada and the US consider these populations the equivalent to species for the purposes of conservation and have assessed their conservation statuses separately. Similarly, at least four recognizably different types of killer whales inhabit the Southern Ocean, there are at least two types in both the North Atlantic and the northwest Pacific, and there are likely a good many more to be discovered. Many of these populations feed on different prey, making a one-size-fits-all set of conservation prescriptions impossible. Identifying these groups genetically and determining their at-sea ranges, numbers, population trends, feeding habits and threats will be a major challenge for conservation managers for many years to come.

Fortunately for killer whales, their relatively small size and low oil yields always made them less attractive to whalers who preferred their larger kin. That said, the species has not been entirely ignored. Japanese whalers took 60 killer whales per year between 1948 and 1957, and the Soviet whaling fleet took four to five per year in Antarctica between 1947-1972 and approximately 900 in the same area in an exceptional hunt in the 1979-1980 season. Although the International Whaling Commission has no records of killer whales being taken commercially since 1982, Scott Baker and colleagues genetically identified killer whale meat in Japanese and Korean markets in 2000, so there may still be some undocumented hunting. Alternatively, the meat may have come from animals acquired as bycatch in fishing operations.

In contrast to relatively limited harvesting of killer whales by commercial whalers, indiscriminate shooting of the species was common throughout the mid-twentieth century, which may have had a much greater impact on some populations. Whalers tended to view killer whales as competitors and some felt it was their duty to kill them when the opportunity presented itself. In British Columbia and Alaska, commercial salmon fishermen also considered killer whales arch competitors and up to the 1970s often drove them away – and occasionally killed them – with gunfire. In the late 1950s in British Columbia, the government mounted a machine gun in a narrow channel (Seymour Narrows) with the intent to eliminate the 'blackfish' that competed with local sports fishermen for salmon. Fortunately, the whales were not seen in the area for some time, the call for a cull subsided, and the gun was never fired. Incidental killing was rarely documented and is therefore difficult to quantify. In Norway, however, records were kept of systematic culls between 1938 and 1981 which accounted for the death of a reported 2, 345 killer whales.

Beginning in the late 1960s, human attitudes began to change and the harassment and culling of killer whales was replaced, in some areas, by live captures for aquariums and oceanariums. Initially, the majority of animals came from the coastal waters of Washington State and southern British Columbia. When government regulators put the brakes on further harvests in that area in the early 1970s the attention of whale capturers turned to Iceland, and later to Japan and Russia. While the number of killer whales taken in live-capture operations has been small, relative to killer whale

Fish out of water? Despite the silly staging, captive killer whales still manage to be breathtaking, inspiring both awe and ire from the public. Photo by Tory Kallman



A broken family: killer whales on the deck of a Soviet whaling factory ship, waiting to be processed. Photo courtesy A. Burdin

numbers worldwide, it certainly had a significant effect on at least one population. Between 1962 and 1974, 68 were taken from Washington and British Columbia, 47 of which are known or believed to have belonged to the now-endangered southern resident killer whale population. Only 70 southern residents were left by 1974, and almost 40 years later, this population still has less than 90 members.

Times have changed, as have the range of threats that killer whales currently face. Ironically, they are now at risk of being "loved to death" in some areas because of a human passion to observe them at close range in the wild. Whale-watching as an industry has exploded in popularity over the last 30 years, with well over 10 million participants per year worldwide. A relatively small proportion of this focuses on killer whales, but in a few areas, for example, around southern Vancouver Island and the San Juan Islands, killer whales are followed by sometimes dozens of vessels, for many hours a day during the whale-watching season.

Current threats to killer whale populations that are arguably much greater than whale-watching and certainly more widespread include environmental contaminants, oil and chemical spills, reduced prey availability, and disturbance and noise pollution by commercial and military activities. And the elephant in the room concerns the effects of climate change, which potentially will impact entire ecosystems - it is pretty much a given that killer whales will be affected by changes in their prey base. Whether their cultural traditions will be flexible enough to adapt remains to be seen.

Killer whales in many parts of the world are highly social and sometimes aggregate in large numbers. This, combined with the fact that they do not appear to avoid noxious substances such as oil, can make large proportions of a population vulnerable to oil or chemical spills. Such was the case in Alaska in 1989, when members of one fish-eating group, referred to as AB pod, were observed swimming through the slick associated with the Exxon Valdez oil spill. Up until the 2010 Deepwater Horizon blow-out, the Exxon Valdez spill was the largest in US history. Within a year of the spill, 13 members of AB pod were dead, a rate of mortality never before witnessed in any well-studied killer whale population. Over 20 years later, this population is still recovering. Members of a second group of killer whales, the mammal-eating ("transient") AT1 population, were also observed swimming in the oil and they have not produced a viable calf since. This population now has fewer than 10 members and is likely doomed to extinction.

More insidious are the effects of other chemical and biological pollutants on killer whales. These may range from antibiotic resistant bacteria and pathogens, to persistent organic pollutants (POPs). Studies have revealed that killer whales in British Columbia and Washington are among the most contaminated mammals in the world. This is likely because killer whales are long-lived, upper trophic level predators, and pollutants such as POPs persist and accumulate over time in their fatty tissues. Concentrations of these fat-soluble pollutants increase with age in male killer whales, but decline in females as they nurse their offspring, the first of which receives much of their mother's lifetime accumulation through her milk. Once the female is no longer reproductive, concentrations then increase at rates similar to male killer whales.

While some "legacy" POPs such as PCBs and DDT have been banned in North America, they are transported through atmospheric processes and ocean currents from as far away as Asia. Killer whales in the remote Crozet Archipelago in the Southern Indian Ocean carry biologically significant accumulations of POPs, showing how widely these contaminants can disperse. Monitoring the sources and levels of environmental contaminants is particularly challenging given that each year, up to 1,000 new chemicals are released into the environment globally. Fire retardants, such as polybrominated diphenylethers (PBDEs), first came into use in the 1990s, and their use increased exponentially. Concern about rising

PBDE levels in human breast milk led to their ban in Europe, as they are persistent, bioaccumulate and are passed along through nursing to children. They are now being banned in other areas of the world. Samples of killer whale blubber collected between 1993 and 1996 showed moderate levels of these contaminants in southern resident and transient killer whales, and it is likely that the whales are carrying a significantly higher contaminant burden now.

Another group of contaminants that may affect killer whales in areas of heavy shipping or intense whale-watching are inhaled pollutants. A recent study by Cara Lachmuth estimated that the heavily POP-contaminated southern resident killer whales off British Columbia and Washington are also inhaling airborne pollutants from vessel exhaust at the threshold of that expected to cause adverse health effects. This problem is exacerbated by calm air conditions during the summer whale-watching season that cause exhaust gases to stratify above the water surface.

Healthy prey populations are critically important to the long-term survival of killer whales, but, it is important to acknowledge that despite their physical ability to hunt for and consume a wide variety of prey, killer whale populations tend to be remarkably narrow and fixed in their prey preferences. The capture of three mammal-eating transient killer whales in 1970 illustrates just how strong these dietary traditions are – after 75 days of refusing to eat the fish they were offered, one of the whales died. Four days later the remaining two whales began to eat fish. When returned to the wild after several months, the surviving whales resumed their diet of marine mammals. In British Columbia, fish-eating resident killer whales primarily target Chinook salmon despite the widespread abundance of other potential prey, including other species of salmon. Studies by Dr. John Ford and his colleagues have recently shown that birth and mortality rates are closely linked to Chinook salmon abundance, pointing to the need for fisheries management plans to incorporate the needs of fish-eating killer whales when considering allocations for fisheries.

There is growing awareness that killer whales are increasingly exposed to physical and acoustical disturbance which may reduce their ability to forage and communicate effectively. We know that background underwater noise has increased significantly (an average of 15 dB) throughout the world's oceans within the last 50 years, and that killer whales in a visually-constrained underwater environment have evolved to use sound in much the same way that terrestrial animals use vision. How chronic noise impacts these activities is not known, but it may add to the suite of stressors that killer whales are exposed to. It is difficult to protect killer whales from increasing noise, as sounds travel much more efficiently and over greater distances in water than in air.

Sources of acute sound, such as airguns used in seismic surveys, military sonars and detonations, or pile driving associated with construction, also have the potential to disrupt killer whales. These sounds can travel from 10s to 100s of km or even further in the case of seismic surveys. In the Atlantic, airguns are the predominant source of chronic anthropogenic noise. Military sonars have been linked to the stranding of beaked whales, and were associated with reports of unusual behavior in of a pod of fish-eating killer whales (J-pod) near the Washington-British Columbia border in 2003. In the later case, after a US navy destroyer activated a commonly used, high intensity, mid-frequency sonar unit, a group of whales approximately 47 km away from the ship reversed direction abruptly. As the vessel overtook them, the pod bunched up, changed directions several times, and finally divided and rapidly left the area in different directions. Up to 100 Dall's porpoises and a minke whale were also seen leaving the area at high speed.

Marine mammal protection laws passed in the US and Canada have meant that there is a lot more prey, including harbor seals, for mammal-eating transient killer whales, and populations of both have increased sharply in recent years. Photo by Dave Ellifrit

In some areas of the world, killer whales have learned to recognize certain sounds associated with commercial fishing as the ringing of a "dinner bell." Changes in engine speed and direction can easily be heard by the whales as longline fishing gear is brought to the surface.

The whales then approach the vessel, and carefully and selectively remove highly valued prey such as sablefish and halibut in Alaska, tuna and swordfish off Brazil, toothfish in the Southern Ocean, and tuna in the Mediterranean. This learned "depredation" behavior can spread quickly through a population and once started, is very difficult to stop. It is also highly costly for the fishers, and in some areas of the world they have tried a range of activities, such as shooting or throwing explosives at the whales, fishing at night, and moving short distances, all of which have failed.

To date the only consistently effective methods to deter depredation are to stop fishing whenever killer whales approach, or in some cases to move large distances (more than 60 nautical miles) when depredation occurs. Changing from hook-and-line gear to pots or traps is also effective, and there has been some success in adjusting the timing of fisheries so that they occur when alternate prey for the killer whales are readily available. The recent development of a "physical depredation mitigation device" (PDMD) that acts as a sleeve to cover hooked fish on a longline as it is drawn to the surface shows promise, although its use is not yet widespread. Hazing and other methods to deter depredating killer whales have had very limited, short-term success. In general, changes in the way that fisheries are conducted are necessary to avoid reinforcing the depredation behaviors. In areas where fisheries depredation is widespread and entrenched for many years, as in parts of the North Pacific and southern Bering Sea, it may, in theory at least, supply sufficient food to lead to growth in killer whale populations. While this might seem to be a net benefit from a conservation perspective, such artificially-augmented populations are highly vulnerable to reductions in fishing effort or changes in fishing methods as described above, and their long-term prospects are almost certainly poor.

Mammal-eating transient killer whales may also be increasing in the northeast Pacific as a result of a different type of human action. The Marine Mammal Protection Act of 1972 brought about blanket protection in US waters of not only killer whales but all of their marine mammal prey. Just a few years prior, culls for harbor seals and sea lions in British Columbia ended, and by 1982 Canada had its own set of Marine Mammal Regulations. In British Columbia, harbor seal numbers have now increased to historic levels. The effect of these actions in both countries is that populations of seals, sea lions and some cetaceans have greatly increased in recent decades, creating improved foraging conditions for these whales.

Human impacts on the ocean are far-reaching, and there is a growing awareness of the need to create areas of refuge for marine animals. Marine protected areas and vessel exclusion zones can help to ease some of the pressures that whales are under. Whale-watching guidelines and regulations are becoming standard fare in many countries, although actual approach distances vary by country, ranging from 50 m in Australia to 100 yards in the US. In British Columbia and Washington State, areas of Critical Habitat have been identified for the fish-eating resident killer whales. These are legally identified areas that seasonally concentrate migratory Chinook salmon that residents rely so heavily on. Planning is now underway to ensure that conservation and protection measures are put in place to protect these areas.

In 1973, the US Navy diving manual warned that killer whales "will attack human beings at every opportunity." This statement was untrue, of course, but the converse is close to the mark: humans are undoubtedly the most dangerous animal on the planet for killer whales. Happily, killer whales now enjoy widespread protection from intentional killing. The challenge at this point is to ensure that our activities in its world – shipping, resource development, fishing, release of pollutants, military testing, etc. – don't have the same effect.

Killer whales head into an uncertain future as we humans increasingly impact marine environments. Photo by Bob Pitman

About Our Authors

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Volker B. Deecke – Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, St. Andrews, Fife, KY16 8LB, Scotland UK. Volker was born in Germany and raised in Austria. He started studying biology in Berlin, but soon transferred to Vancouver where he completed a Masters Degree investigating the evolution of vocal dialects in resident (fish-eating) killer whales at the University of British Columbia. He received his doctorate from the University of St. Andrews in Scotland, focused on the vocal behavior of transient (mammal-eating) killer whales in British Columbia and Alaska and the response of harbor seals to killer whale calls. After post-doctoral research at the University of British Columbia, Volker returned to St. Andrews where he is currently a research fellow at the Sea Mammal Research Unit studying the behavior of killer whales in Scottish waters. Volker's specialty is the underwater sounds of killer whales with a special emphasis on how prey hearing has affected their acoustic communication.

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Christophe Guinet – Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79 360 Villiers en Bois, France. Christophe is part of a marine predator team directed by Henri Weimerskirsh; he is in charge of the marine mammal research program, with a special focus on the influence of oceanographic conditions or human activities on the foraging efficiency of these species and their demographic consequences. Christophe and his students are working on a broad range of marine mammal species ranging from pinnipeds (fur seal and elephant seal), to cetaceans (killer whales, sperm whales, baleen whales). Since the late 1980s, most of his field work has been conducted on the French subantarctic islands (Crozet, Kerguelen, Amsterdam islands).

Killer Whale: Authors

Paul Tixier - Centre d'Etudes Biologiques de Chizé, Centre National de la recherche Scientifique, 79 360 Villiers en Bois, France. Part of Paul's Master's thesis was on northern resident killer whales in British Columbia, and he is now in the last year of a PhD program on killer whale and sperm whale populations off Crozet and Kerguelen islands under supervision of Dr. Christophe Guinet. His work focuses on depredation of longline fisheries and their consequences on the whale populations, with an emphasis on feeding ecology, demography and social organization, as well as the assessment of economic losses and mitigation solutions.

Alisa Schulman-Janiger - Marine biologist/educator in San Pedro High School's Marine Science Magnet for the past 21 years, and on boats for the 10 previous years. She has a Bachelor's of Science degree from California State University, Long Beach in Zoology (emphasizing marine biology). Alisa served as on-board naturalist in Alaska, Baja California, and California, naturalist and staff scientist while researching humpback whales in Massachussetts, and field researcher on harbor porpoise, humpback whales, and killer whales with the National Marine Mammal Lab in Alaska. She trains volunteer naturalists in the Cabrillo Whalewatch Program, and has served on ACS/LA's Board of Directors since 1983, and as director of ACS/LA's shore-based Gray Whale Census and Behavior Project, based at Point Vicente and staffed by trained volunteers. Alisa has been photo-identifying California killer whales and studying their distribution, natural history, and behavior for over 27 years.

Nancy Black- Monterey Bay Whale Watch Center, Monterey, CA. Nancy is a marine biologist who owns and operates Monterey Bay Whale Watch Center in partnership with Richard Ternullo. Nancy has a Masters of Marine Science degree from Moss Landing Marine Laboratories (focusing on Pacific white-sided dolphin). Nancy has been photo-identifying Monterey Bay killer whales and studying their distribution, natural history, and behavior for over 22 years. She worked as the primary investigator for the Oceanic Society's whale and dolphin research program. She has done spotted dolphin research off the Bahamas, aerial surveys of marine mammals off California with Cascadia Research, and field research on Alaskan killer whales with the National Marine Mammal Lab.

Richard Ternullo - Monterey Bay Whale Watch Center, Monterey, CA. Richard owns and operates Monterey Bay Whale Watch Center in partnership with Nancy Black. He graduated from San Diego State University in 1972 with a degree in microbiology, obtained a Captain's License, and has been operating fishing and natural history trips on Monterey Bay for 39 years. He teaches classes devoted to seabird ecology and identification, and served as president of the Monterey Bay Chapter of ACS. Richard has collected data on all the cetaceans encountered on Monterey Bay since 1982. He operates a marine mammal sighting network involving many boats, compiling and regularly reporting in Monterey Bay Whale Watch's Sightings summary. He has a keen interest in killer whales and their predatory behavior and prey interactions, especially for transient killer whales.

Lance G. Barrett-Lennard - Cetacean Research Lab, Vancouver Aquarium Marine Science Centre, PO Box 3232, Vancouver, B.C., V6B 3X8, Canada, and Zoology Department, University of British Columbia, #2370-6270 University Blvd., Vancouver, B.C. V6T 1Z4, Canada. Lance is Head of the Cetacean Research Lab at the Vancouver Aquarium and an adjunct professor in the Zoology Department at the University of British Columbia. His research focuses on feeding ecology, population structure, mating systems, and cultural transmission in cetaceans, particularly killer whales. He has conducted field studies in British Columbia and Alaska since the late 1980's and supervises an eclectic crop of graduate students working on topics ranging from harbor porpoise population structure to vocal learning in belugas.

Robin W. Baird - Cascadia Research Collective, 218 1/2 West 4th Avenue, Olympia, Washington 98501, USA. Robin is a Research Biologist with Cascadia Research Collective, a non-profit research and education organization based in Olympia, Washington. He first began working with killer whales in 1985, volunteering to collect killer whale photos for Mike Biggs' population monitoring efforts in British Columbia. In 1988 he began graduate work at Simon Fraser University in Burnaby, B.C., focusing on foraging behavior and ecology of mammal-eating killer whales. He completed his Ph.D. in 1994, and while he spends most of his time working with various tropical odontocetes, he has continued studies of killer whales in the Pacific Northwest and elsewhere.

Kathy Heise - Vancouver Aquarium Marine Science Centre, PO Box 3232, Vancouver, B.C., V6B 3X8, Canada. Kathy is a self-employed marine biologist and a Research Associate at the Vancouver Aquarium. Her current research is on echolocation use by cetaceans and she has a strong interest in the effects of underwater noise on marine life. She has been involved with marine mammal research for over 25 years in both British Columbia and Alaska, with a particular emphasis on Pacific white-sided dolphins and killer whales.

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