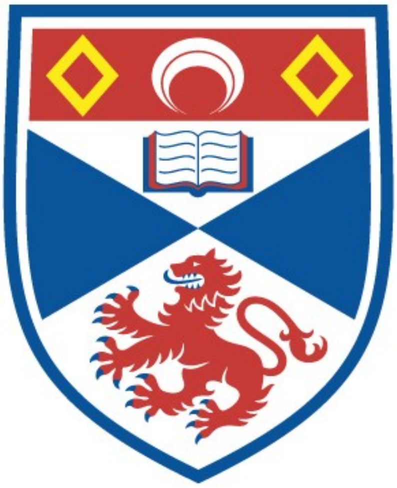

THE VOCAL BEHAVIOUR OF TRANSIENT KILLER WHALES (*Orcinus orca*): COMMUNICATING WITH COSTLY CALLS

by

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Submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy, University of St. Andrews

April 2003

ABSTRACT

Killer whales in the northeastern Pacific exhibit dietary specialisation and are segregated into fish-eating *resident* and mammal-eating *transient* populations. The aim of this study was to examine the vocal behaviour of the West Coast transient population and compare it to information on sympatric fish-eating killer whales from the literature. I describe and test an automated system for the categorisation of vocal patterns that, by addressing important features about the perception of sound, attempts to circumvent some of the shortcomings of previous methods. The analysis of the behavioural context and the frequency of occurrence of vocal activity in transient killer whales found that transients vocalise less frequently than residents and do so only in a few narrowly defined contexts. In order to determine whether this difference is due to the fact that transient killer whales hunt acoustically sensitive prey, I played killer whale calls to harbour seals. The seals responded to the calls of transient killer whales by diving, but did not respond to the calls of familiar fish-eating killer whales. Seals responded strongly to unfamiliar calls of fish-eating killer whales from Alaska, which shows that the difference in response is the result of learning and experience. Finally, I used the automated categorisation system to analyse repertoire variation among West Coast transient killer whales. Repertoires showed little variation between different regions and social groups, in contrast to sympatric fish-eating populations, and all members of the population share a number of call types. By comparing the vocal behaviour between populations of animals that are nearly identical in many aspects of their biology, yet differ strikingly in a few, this study has shed light on some of the factors that exert influences on the context and nature of vocal communication.

DECLARATION

I. I, Volker B. Deecke, hereby certify that this thesis, which is approximately 34000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

18 April 2003
Date
Signature of Candidate

II. I was admitted as a research student in January 1999 and as a candidate for the degree of Doctor of Philosophy in Biology in January 2000; the higher study for which this is a record was carried out in the University of St Andrews between 1999 and 2002.

18 April 2003
Date
Signature of Candidate

III. I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy (Biology) in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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ACKNOWLEDGEMENTS

Obtaining insights into the lives of highly mobile animals such as killer whales that range over vast areas requires researchers to work in teams. No single person can hope to map the range and document the entire variation in behaviour and ecology of such nomadic species. All good research in the field of marine mammal biology is therefore the result of effective teamwork, and, although its merit remains to be tested, this thesis likewise is the product of many rather than just myself.

First and foremost I would like to thank the two people who were most instrumental in making this project happen. Peter Slater I thank for investing sufficient faith in me to allow me to embark on this risky undertaking. Peter has taught me to think like an ethologist rather than a marine mammal scientist and to see the many parallels between the behaviour of animals as diverse as chaffinches and killer whales. John Ford was equally important in making this study a reality. John shared his immense knowledge on acoustic communication and behaviour of killer whales and provided invaluable advice, logistic support, local knowledge and access to a life-time collection of recordings of transient killer whales without all of which this study would not have been possible.

Although I did not have the opportunity to meet him, I feelindebted to Michael Bigg. Mike was a pioneer in the research of killer whales in the wild and has laid down a very solid foundation for the study of the ecology and behaviour of these animals. I feel that without Mike's vision and contagious enthusiasm, we would know very little about wild killer whales today. His premature death in 1990 was a great loss for all of us.

Research on killer whales off the West Coast of North America today would be dead in the water if it was not for the tireless efforts of Graeme Ellis. Graeme is probably the only person in the world who can identify some 600 members of another species from tiny nicks and scratches on their backs. If it was not for Graeme's help identifying which individuals were present during different encounters with transient and resident killer whales, most of the results presented in this thesis would be meaningless and I am very grateful for his patiently answering my many inquiries.

The top floor of St. Andrews University's Bute Biomedical Building has been a fabulous place to work, as well as a hot house of animal behaviour where much of this thesis grew. I felt welcome from the start and I consider myself very fortunate for the friends I have made there. I would like to thank my fellow members of the Bird and Mammal Sound Communication Group, Vincent Janik, Rob Lachlan, Nigel Mann, Lorraine Marshall-Ball, Susanne McCulloch, Hugo Rainey, Alison Rutstein, Ari Shapiro, Sally Ward, and Mel Wohlgemuth for providing ideas, feedback and constructive criticism on many aspects of this research. The other inhabitants of 'The Bute' were equally important: Mike Ritchie and Jeff Graves provided helped with statistics and biological concepts. Jon Evans, Jen Kelley, and Clive Nuttman provided stimulating discussion and gourmet sustenance. Simon Potts was instrumental in making the Bute such a great social environment. Thanks to you, Potts, for organising the many parties, a well as the annual trips to Glenelg. Su Engstrand, Leon Hockham, Natasha Lebas, Mark Lineham, Anna Ludlow, Kit Magellan, Guđbjörg Olafsdottir, Lucy Gilbert, Lars Pettersson, Miguel Serrano, Emma Smart, Joe Tomkins, Betsy Vulliamy and Shane Webb and many other Butees all provided helpful advice and ideas, usually over coffee or a pint at the pub.

I would like to thank the members of the Behaviour Discussion Group at St. Andrews University for their comments and suggestions. The group has provided an valuable forum for presenting ideas and obtaining feedback on work in progress. Special thanks go to Richard Byrne, Jeff Graves, Phil Hammond, John Harwood, Andy Whiten, as well as to Vincent Janik, Nigel Mann, Peter Slater and Klaus Zuberbühler for organizing the group meetings. I would furthermore like thank Len Thomas at St. Andrews University for his frequent help with statistical problems, a well as for providing fruit smoothies and accommodation when I returned from field work without prior arrangements.

In Vancouver, the Cetacean Research Lab at the Vancouver Aquarium provided a place to analyse data, as well as much helpful support and feedback. Special thanks go to Lance Barrett-Lennard for his help with field logistics and for

many fruitful discussions. Harald Yurk similarly provided much invaluable help, ideas, as well a comments on many aspects of this research. Thanks also to Nic Dedeluk, Kerry Irish, Sheryl Knoedler, Michaela McDonald, Nancy Marcus, Doug Sandilands, Chris Tucker, and Valeria Vergara for their company and feedback. At the University of British Columbia, I want to thank Pamela Rosenbaum for logistic support in printing this thesis. Lance Barrett-Lennard, Emma Bredesen, Madlen Denoth, Ed Gregr, Sheila Heymans, Kristin Kaschner, Dave Rosen, Dom Tollitt, Valeria Vergara, Ben Wilson, Arliss Winship, and Harald Yurk read drafts of this thesis. Their combined editing skills greatly improved the quality of the final document.

I'm indebted to all the people who helped with the field research for this study. Field budgets were often tight and many people helped to stretch them further. In Alaska, Dena Matkin played a crucial role in supplying boat time, hospitality, tremendous local knowledge and help in the field. I'm especially grateful to Dena for introducing me to the beauty of Glacier Bay National Park. Craig Matkin, Eva Saulitis and Harald Yurk also provided essential help with field work here. Furthermore, I would like to pass on a big thanks to the staff at Glacier Bay National Park for their logistic support and for passing on killer whale sightings.

In British Columbia I would like to thank Graeme Ellis for his help with field logistics. Graeme organised boats, taught me everything I know about outboard engines and navigation, provided much valuable information on the distribution of harbour seals and killer whales, and lent a hand whenever needed. Similarly, Jane Watson was a great help with many aspects of this study. John deBoeck and Bobbie and Ruth Lamont generously provided accommodation in the trapper shack at Clam Cove. Thanks go to Peter Arcese and the Tseycum and Tsawout Indian bands for letting me use the research facilities on Mandarte Island. Rob Williams made his cabin on Pearse Island available whenever it was needed and also provided many good suggestions, help in the field and use of his boat.

Jim and Mary Borrowman and everyone at Stubbs Island Whalewatching provided invaluable logistic help in the field, hospitality in Telegraph Cove and a steady flow of information about whale sightings in the area. Similarly Bill and

Donna Mackay of Mackay Whalewatching offered hospitality in Port McNeill and supplied much information on killer whale movements. Alex Morton provided accommodation and hospitality in Echo Bay and shared her knowledge about seal haulouts and killer whale movements in the Broughton Archipelago. Markus Kronwitter went to extra lengths to make a stay at Malei Isle Lodge pleasant and successful.

A special thank you goes to everyone who helped me in the field, who put up with long hours of boredom interspersed with sporadic bouts of frenzied activity, with malfunctioning playback and recording equipment, rain, sun, wind and cold in order to help with the research. Without your great support and company this study would not have been possible. Claire Brignall, Nicola Dedeluk, Manfred Enstipp, Dena Matkin, Patrick Presi, Eva Saulitis, Anna Spong, Shawn Taylor, Gunna Weingartner, Rob Williams, Mandy Wong, and Harald Yurk all helped with the field work.

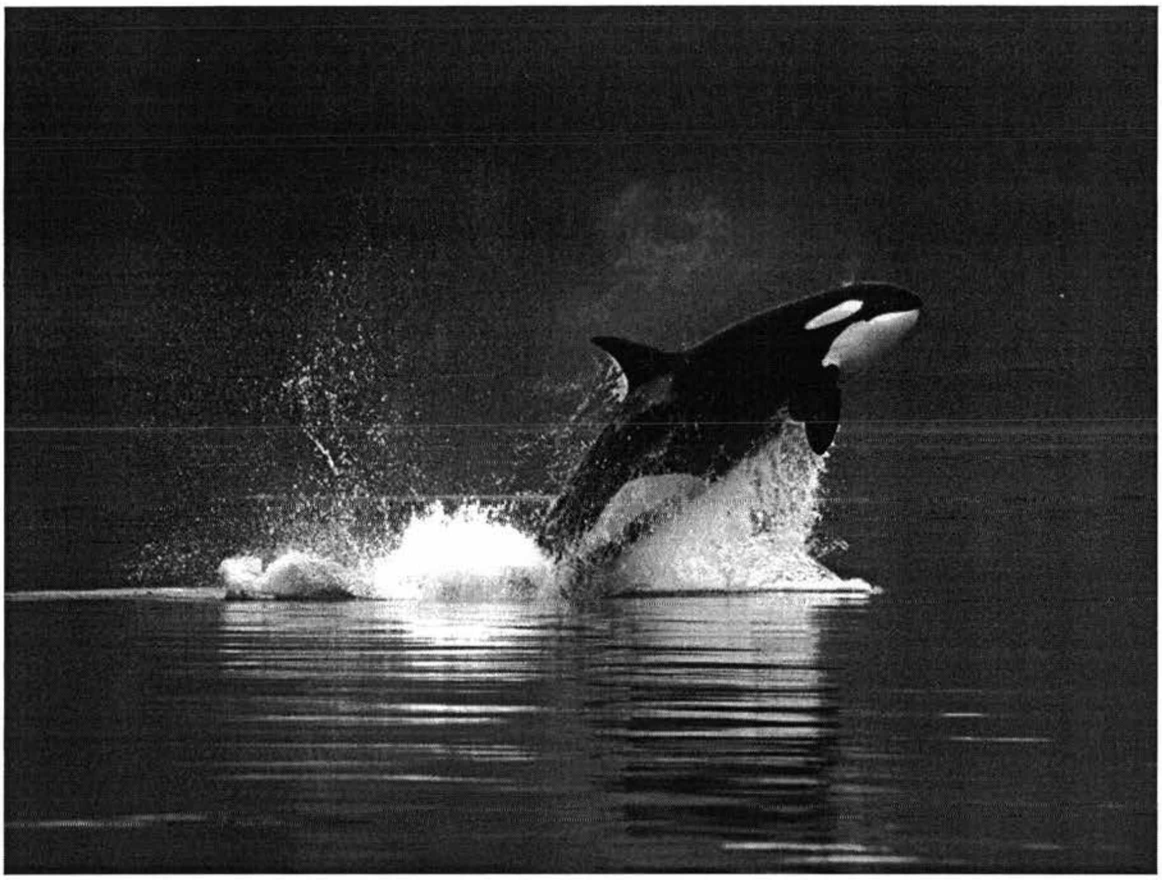
The foundation of this study is a database of recordings of transient killer whales covering the entire known range of this population from California to Southeast Alaska. Almost every researcher who recorded a sound from these animals has made their recordings available to me. I am very grateful for this contribution and hope that this study will underscore the importance of the spirit of collaboration among killer whale researchers along the West Coast. Thank you to Nancy Black, Robin Baird, Leo Beranek, Michael Bigg, Richard Bolt, Jim Borrowman, Randy Burke and the crew of the SV *Island Roamer,* Kechura Davidson, Graeme Ellis, Brian Falconer and the crew of the SV *Maple Leaf,* Bev Ford, John Ford, Chris Gabriele, Dawn Goley, Rolf Hicker, Rick Hobbs, Jeff Jacobsen, Bill Mackay, Charles Malme, Dena Matkin, R. Mlawski, Alexandra Morton, Robert Newman, Linda Nichol, Rod Palm, Greg Silber, Eva Saulitis, Paul Spong, Dan McSweeney, Helena Symonds, Rich Ternullo, and Frank Thomsen. In addition I am very grateful to John Ford, Malene Simon, Fernando Ugarte, Harald Yurk, and everyone at the Center for Whale Research, but especially Candi Emmons and Ken Balcomb, for their contribution of recordings of fish-eating killer whales for the playback experiments.

Funding for the field component of this study came from the Vancouver Aquarium Marine Science Centre and I am very grateful for their efforts to further our knowledge about the marine environment. Funding also came from the Wild Killer Whale Adoption Program. I would like to thank all members for their contributions. The BBC's Natural History Unit funded additional field work in Alaska and special thanks go to Sue Flood and Doug Allan for inviting me to join them. National Geographic funded a crucial field trip to the Gordon Islands - thanks go to Douglas Chadwick and Flip Nicklin for this opportunity. During part of my stay in Scotland, I was supported by a Doktorandenstipendium aus Mitteln des Dritten Hochschulsonderprogramms, and I am indebted to the German Academic Exchange Service for giving me this opportunity. The framework for the neural network algorithm for call categorisation is based on computer code supplied by Aaron Garrett.

During the last four years I have received tremendous support from many friends and from my family. Being able to rely on this help is what kept me going during this often fun, and sometimes challenging time. A big thank you to my parents Lüder and Gertraud, and to my brothers Ulf and Arved, for all their help and their love. Living in Scotland was a wonderful opportunity to tighten the bonds with my god-parents, Michael and Maggie Moss, and their children Sarah, Susannah and Alexander. I consider myself very privileged to have such a splendid second family. I am very fortunate to consider Lance Barrett-Lennard, Alistair Blachford, Graeme Ellis, Manfred Enstipp, John Evans, John Ford, Brian Gisborne, Kristin Kaschner, Jen Kelley, Mikis Manolis, Monique Trepanier, Len Thomas, Marc Wen, Hal and Linda Weinberg, Rob Williams, Harald Yurk, and Pablo Yuste as great friends. Your friendship has been a tremendous help and enrichment for me. Last on paper but always first in my mind, I would like to say a very special thanks to Gunna Weingartner for her help and support in the field and at home, and to my daughter Lina for being the sweetest distraction in the world.

DEDICATION

I dedicate this thesis to my daughter Lina who, in the last ten months, has taught me a great amount about the importance of acoustic communication. I am anxious to watch your communication skills develop and unfold and hope that the communication between us will always be clear and promote mutual understanding. But most of all, I cannot wait to hear you call my name.



Female transient T086 breaching in Icy Strait, Southeast Alaska

CHAPTER I - General Introduction

1 The Benefits and Costs of Acoustic Communication

In acoustic communication, an animal uses sound patterns to transmit information so that on average the sender benefits from the response of the receiver (Slater 1999). While acoustic communication may increase the fitness of the sender, the receiver will usually only modify its behaviour if it too benefits from doing so. Communication is therefore often mutualistic. The benefits of vocal communication can be substantial: a male treefrog, cricket, or songbird using vocal signals to attract females can secure an opportunity to mate and thus ensure that his genes are transmitted to the next generation. A juvenile bird can increase its food intake substantially by issuing begging calls and thus ensure its own survival. Under the threat of predation, group-living animals can attract conspecifics by vocalising and thus increase their own chances of survival through safety in numbers.

The large potential benefits of acoustic communication are offset to some degree by its associated costs. Much research has investigated the energetic costs for sound production in many species of insects, amphibians, mammals, and birds. These energetic costs are substantial in many species of insects and amphibians, equalling or exceeding the cost of terrestrial locomotion in these animals (see Prestwich 1994) and, in some cases, exceeding the energy that can be supplied by aerobic metabolism (Pough & Gatten 1984). By contrast, the energetic costs for vocal behaviour were found to be small in endothermic species such as birds (Chappell *et al.* 1995; Horn *et al.* 1995; Oberweger & Goller 2001; Ward *et al.* in press), with metabolic rate during vocal activity being only 1.02 and 1.36 times that while resting or perching silently (compared to a 23 to 28 fold increase of metabolic rate during intermittent powered flight; Tatner & Bryant 1986; Nudds & Bryant 2000). Jurisevic *et al.* (1999) report somewhat higher energetic costs for begging and distress calls in juvenile and adult birds (1.2 to 4.9 times resting metabolic rate, but see McCarty 1996); however, these costs are still small compared to those for other activities. Aside from humans where the cost of speech is relatively small (oxygen consumption is at or below resting levels for quiet and comfortable speech and at 1.06 to 1.22 times resting level for loud speech; Russell *et al.* 1998), few studies have looked at energetic costs for vocal communication in mammals. Bats that forage on the wing experience minimal costs for the production of echolocation calls, since the sound production mechanism appears to be partly driven by the wing musculature (*e.g.*, Speakman & Racey 1991; Arita & Fenton 1997; Wong & Waters 2001).

Aside from these proximate costs resulting from the energetic requirement of sound production, vocal behaviour in many cases generates indirect fitness costs by transmitting information to unintended receivers. Such indirect costs have been investigated in many animals that, by vocalizing, reveal their location to potential enemies. The same features that make acoustic signals effective for transmitting information between animals in communication, such as the fact that they allow communication over large distances and in habitats where vision is limited, make them potentially dangerous for these animals to use. For example, insects using acoustic displays to attract a mate also run the risk of attracting bats (*e.g.*, Hosken *et al.* 1994) or parasitoid flies (Lehmann & Heller 1998; Müller & Robert 2002). Begging calls used by juvenile birds to stimulate food provisioning by the parents have the negative side-effect of revealing the location of the nest (Haskell 1994). In many species, begging calls therefore have low amplitudes and high frequencies making them difficult to locate (Briskie *et al.* 1999). Vocal signals used in intersexual communication in birds, either to coordinate behaviour between members of a pair (*e.g.*, Yasukawa 1989) or to attract a mate (*e.g.*, Mougeot & Bretagnolle 2000) can similarly increase the risk of predation. Paradoxically, in a few species, male birds actually increase their vocal displays when hearing predator calls (Langmore & Mulder 1992; Zelano *et al.* 2001). In many species, the indirect fitness costs of vocal communication from revealing information to predators or parasitoids therefore far exceed the fitness cost from using energy for sound production.

Not only prey, but also predators can pay a high price for vocal communication: predators that hunt animals with good hearing abilities and that rely on stealth and surprise to overcome their prey can decrease their hunting success substantially by vocalizing and thus giving away their location. Like the male cricket that uses acoustic communication to attract a mate and thus to increase its fitness, yet at the same time risks attracting a parasitoid fly that could kill it prematurely and so greatly reduce its lifetime reproductive success, predators of acoustically sensitive prey are caught in a similar dilemma between the benefits and costs of transmitting information using acoustic signals. These costs have been examined in bats, whose echolocation calls are audible to some species of insects, which has lead to a sensory arms race between the hearing capability of the prey and the frequency for echolocation used by the predator (e.g., Fenton & Fullard 1981). Aside from this remarkable system, the available information on ecological costs of vocal behaviour in predatory animals is exceedingly sparse.

The vocal communication of killer whales (*Orcinus orca*) provides a fascinating opportunity to investigate the indirect, or ecological, costs for vocal communication in a predatory species. The largest members of the dolphin family, killer whales are top predators in the marine ecosystem, and live in a habitat where visual and olfactory communication are extremely limited. Due to low attenuation and fast speed of sound in water, the aquatic environment provides an excellent medium for transmitting information using acoustic signals. As far-ranging social animals with a need for long-range communication, killer whales and most other toothed whales rely largely on acoustic signals for navigation and communication. In addition, as explained below, different populations of killer whales in the northeastern Pacific differ drastically in the indirect costs they pay for vocal communication. This offers a rare opportunity for a comparative approach to delineate the role of such costs in shaping systems of acoustic communication.

2 Sound Production in Dolphins and Porpoises

The mechanism of sound production in toothed whales differs drastically from that in terrestrial mammals and is thought to have developed independently after the evolution of an aquatic existence. Unlike terrestrial mammals that produce vocalisations in their larynx, toothed whales produce sounds in the upper nasal tract, between the dorsal apertures of the bony nares and the blowhole (e.g., Amundin & Andersen 1983; Norris 1986; Cranford 1988). The larynx appears to play no role in the generation of sounds. As a consequence the facial anatomy of dolphins (Delphinidae) and porpoises (Phocoenidae) shows striking differences compared to that of terrestrial mammals: two connective tissue structures, called the nasal plugs, constrict the nasal passage just above the bony nares. The nasal tract is surrounded by four paired air sacs, the nasal sacs. Two pairs of nasal sacs (premaxillary and posterior sacs) lie below the nasal plugs, the remaining two (vestibular and nasofrontal sacs) are situated above the plugs (Cranford 1988; Curry 1992; Cranford *et al.* 1996).

It is thought that during sound production, the muscle complex surrounding the bony nares and the premaxillary and posterior sacs contracts to force air past the nasal plugs into the vestibular and nasofrontal sacs. This ultimately leads to vibrations of the nasal plugs, the site of sound generation (Dormer 1979; Amundin & Andersen 1983; Curry 1992; Cranford *et al.* 1996). The position of the plugs in the nasal passage appears to be under neuromuscular control, since air pressure alone is insufficient to generate sound (Amundin & Andersen 1983). The air can subsequently be recycled so that sound production is independent from inhalation and exhalation (Dormer 1979).

Studies using cineradiography on vocalising animals suggest that in dolphins the two nasal plugs are used to produce different types of vocalisations: the results show that the right nasal plug functions to generate echolocation clicks, while the left nasal plug is used to produce whistles (Dormer 1979). Asymmetries in the morphology of the skull and facial tissues to allow efficient generation and propagation of the two different types of vocalisations are consistent with this finding (Cranford *et al.* 1996). Porpoises only produce echolocation clicks and not whistles and do not use the left nasal plugs to produce vocalisations of any type (Amundin & Andersen 1983).

The melon, a fatty tissue lies immediately anterior of the nasal plugs is thought to act as an acoustic lens. Differences in the density of the fatty tissue generate a velocity gradient for sound waves passing through the melon, which has the effect of focussing high frequency sounds (Aroyan *et al.* 1992; Cranford *et al.* 1996). This focussing effect enables dolphins and porpoises to project much of the sound energy for echolocation and communication forward and is responsible for the high degree of directionality in the high-frequency components of echolocation clicks and communicative vocalisations of these animals (e.g., Schevill & Watkins 1966; Miller 2000b; Lammers *et al.* 1993).

3 Killer Whale Populations in the Northeastern Pacific

Killer whales of the northeastern Pacific are among the best-studied populations of large mammals in the world. Individual killer whales can be consistently identified from the shape of their dorsal fin and the grey patch behind the fin called the saddle patch, as well as from scars and nicks on their dorsal fins and flanks (*e.g.*, Bigg 1982; Bigg *et al.* 1990). Studies using photographic identification of individuals began in the early 1970's off the coast of British

Columbia, Canada, as well as adjacent Washington State, USA, and have provided a wealth of information on the behaviour, genealogy, and social interactions of individuals. These studies soon indicated that two distinct forms of killer whales, that differ in many aspects of their behaviour, social organisation and ecology, inhabit these waters (Bigg 1982; Felleman *et al.* 1988).While these early studies are largely anecdotal, their findings have since been substantiated by 30 years of research into the social organisation, behaviour, ecology and population genetics of killer whales in the northeastern Pacific.

The two forms of killer whales, traditionally but not particularly descriptively called *resident* and *transient*, show striking differences in their diet, and this difference has implications for nearly all aspects of their life-history, behaviour, and social organisation. Results of a long-term study involving the recovery of prey remains from photographically identified individuals, as well as analysis of stomach contents from stranded animals, have shown that resident killer whales feed exclusively on fish, while transients only take marine mammals and occasionally sea birds (Ford *et al.* 1998). Resident killer whales focus on the five species of Pacific salmon (*Oncorhynchus* spp.) with a preference for chinook salmon (*O. tshawytscha*), and their movement patterns are closely tied to the migration of salmon into coastal waters in summer and fall (Nichol & Shackleton 1996). Transient killer whales predominantly feed on pinnipeds and small cetaceans including harbour seals (*Phoca vitulina*), sea lions (*Eumetopias jubatus* and *Zalophus californianus*), northern elephant seals (*Mirounga angustirostris*), harbour porpoises (*Phocoena phocoena*), Dall's porpoises (*Phocoenoides dalli*), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Transient killer whales also attack some of the larger baleen whales including grey whales (*Eschrichtius robustus*; Baldridge 1972; Goley & Straley 1994) and minke whales (*Balaenoptera acutorostrata*; Hancock 1965; Ford *et al.* 1998). Sympatric populations of killer whales that differ in their dietary preference have also been reported from southern Alaska (Saulitis *et al.* 2000), as well as from Antarctic waters (Berzin & Vladimirov 1983).

Resident killer whales live in extremely stable matrilineal kin groups. The nuclear unit of resident killer whale society is the matriline, which consists of a female and her offspring. Permanent dispersal of male or female offspring from the maternal group appears to be completely absent in the resident populations (Bigg *et al.* 1990). Because killer whales are long-lived (average life expectancy for females: 50.2 years; for males 29.2 years; Olesiuk *et al.* 1990), matrilines often contain three, and sometimes four generations. Only after the oldest female dies do her daughters, who by then usually have offspring of their own, start travelling apart. This split is very gradual, and siblings whose mother has died may still spend the majority of time associated. All matrilines that have been seen travelling together make up a community (Bigg *et al.* 1990). The resident killer whales of British Columbia, Washington State, and southern Alaska belong to two distinct communities. The northern resident community ranges from central Vancouver Island north into Southeast Alaska (Ford *et al.* 2000). In the northern part of this range, its members have occasionally been seen travelling together with Alaskan residents, which travel the waters of Southeast Alaska and Prince William Sound west to Kodiak Island (Dahlheim *et al.* 1997; Matkin *et al.* 1999). Northern and Alaskan residents therefore form a common community with two distinct subcommunities. The southern resident community inhabits the waters of

Washington State and British Columbia south of central Vancouver Island and its members have been sighted as far south as Monterey Bay, California (Ford *et al.* 2000). Members of the southern and northern resident community have never been seen to associate.

Since its members range over a greater area and individuals are often not sighted for several years, less is known about the social organisation of transient killer whales. Their social structure is also organised along maternal lines, and some individuals consistently travel with their mothers into adulthood. Others, including both males and females appear to permanently disperse from the maternal group (Bigg *et al.* 1990; Baird & Whitehead 2000). In this respect, therefore, the social structure of the transient population resembles the fission-fusion societies of other delphinids, and offers the opportunity for extensive contact between individuals that are not closely related along maternal lines.

As with resident killer whales, communities of transient killer whales include all animals that have been seen travelling together (or with common social partners). The known range of the West Coast community of transient killer whales extends from Monterey Bay in central California to Glacier Bay in southeast Alaska. While some of its members have only been sighted in a small part of this range (*e.g.*, Ford & Ellis 1999), others have been seen in most parts of the range (Goley & Straley 1994; Ford & Ellis 1999). To the north, the range of the community of West Coast transients borders on that of the Gulf of Alaska transients. Members of this community are on rare occasions seen in the inshore waters of Southeast Alaska, and it is not clear whether they associate with members of the West Coast transient community. A small, isolated community of mammal-eating killer whales currently numbering only 11 individuals inhabits the waters of Prince William Sound in southern Alaska. This community has not produced a viable calf in over 15 years and are likely to go extinct (Matkin *et al.* 1999; Saulitis *et al.* 2000; Scheel *et al.* 2001).

Three studies have used molecular genetics to investigate the population structure and evolutionary history of killer whales in the northeastern Pacific. Hoelzel & Dover (1991) and Hoelzel *et al.* (1998) found highly significant genetic differentiation at nuclear and mitochondrial loci between resident and transient killer whales. A comparison between parapatric resident populations (northern and southern residents) showed a small but fixed difference in the mitochondrial DNA. These results suggest that fish-eating and mammal-eating killer whales have been reproductively isolated for many generations and that different resident populations represent maternal lineages. Using additional markers and a far greater sample size of identified individuals from different resident and transient populations, Barrett-Lennard (2000) showed that fish-specialists and mammal-specialists represent monophyletic groups, suggesting that the differentiation between the two killer whale ecotypes in the northeastern Pacific occurred only once. Barrett-Lennard (2000) also found that the population of fish-eating killer whales in southern Alaska shows two mitochondrial haplotypes. One of these haplotypes is identical to that of the northern resident population of British Columbia, the other to that of the southern resident population of British Columbia and Washington State. The two killer whale ecotypes in the northeastern Pacific have not interbred for many generations, but both residents and transients have produced viable offspring with Icelandic killer whales in captivity (Barrett-

Lennard 2000). This suggests that the mechanism of reproductive isolation is strictly behavioural mechanisms and that the two forms should arguably be considered as belonging to the same species.

4 Acoustic Behaviour of Northeastern Pacific Killer Whales

The vocal behaviour of resident and transient killer whales consists of three types of vocal signals (Ford 1989). Clicks, short pulses of sound that are usually produced in series, function in echolocation for orientation and prey capture (Awbrey *et al.* 1982; Barrett-Lennard *et al.* 1996). Whistles are tonal signals with little or no harmonic content and typically range in frequency between six and 12 kHz (Awbrey *et al.* 1982; Ford & Fisher 1982; Ford 1989). Whistles tend to be most common in social contexts (Ford 1989; Thomsen *et al.* 2002). Some whistles of resident killer whales are highly stereotyped and stable over many years (Thomsen *et al.* 2001).

The majority of killer whale vocalisation falls into the third category of pulsed sounds (Ford & Fisher 1982; Ford 1989). Due to the high pulse repetition rates (between 0.1 and 4.5 kHz), pulsed calls have distinct tonal properties. Many pulsed calls contain an overlaid upper frequency component (at 6-8 kHz), which is not a harmonic of the pulse repetition rate. The upper frequency component is highly directional and therefore could signal the orientation of a calling whale (Schevill & Watkins 1966; Miller 2000b). The mechanism responsible for the generation of the two components of pulsed calls is poorly understood. In some call types such as WCT12 (see Appendix III) the upper frequency component ends before the lower frequency component, which implies that the components can be produced independently of each other. Combined with the fact that the two components are not harmonically related, this suggests that two independent sound generators, possibly the two nasal plugs, are involved.

Ford & Fisher (1982) and Ford (1989) grouped pulsed calls into three categories. *Discrete* calls are stereotyped and can be categorised into different call types according to their structural properties. 70 to 95% of pulsed calls fall into this category (Ford & Fisher 1982). *Variable* calls are not stereotyped and cannot be divided into clearly defined call types. Finally, *aberrant* calls are structurally based on a discrete call type, but show some degree of modification. Like whistles, these tend to occur most frequently during social interactions (Ford 1989).

Ford (1989; 1991) and Yurk *et al.* (2002) studied repertoire variation in resident killer whales at the level of the pod, a group of presumably related matrilines. They found that resident pods have a vocal repertoire of seven to 17 different discrete call types. Ford (1989; 1991) showed that captive individuals produced all call types in their group's repertoires. Call repertoires therefore represent true group dialects, and are not merely the sum of the individual signatures of a group's members. Ford (1989; 1991) also found that certain call types are shared among pods, and that different pods produce consistently different versions, or subtypes, of these shared call types. An acoustic clan includes all pods that share at least one call type.

The northern resident community contains three such clans, whereas the southern resident community is comprised of a single acoustic clan (Bigg *et al.* 1990; Ford 1991). The resident killer whales from southern Alaska fall into two acoustic clans. These differ at a single locus of their mitochondrial DNA suggesting that clans represent maternal lineages (Yurk *et al.* 2002). Matrilines from different clans within the same population still frequently associate and interact socially, although they have no call types in common. Strager (1995) has since described a similar system of repertoire variation from killer whales in the waters off northern Norway, which suggests that the presence of group-specific vocal repertoires is not unique to eastern Pacific killer whales, but may be characteristic of the species as a whole.

The complexity in variation of stereotyped calls in killer whales is most parsimoniously explained by vocal learning. Bain (1986; 1988) provides an account of a female Icelandic killer whale mimicking the calls of a northern resident female in captivity. A similar account of vocal mimicry comes from the Vancouver Aquarium (John Ford, *pers. comm.*) where a male northern resident killer whale started copying the calls of a southern resident female and subsequently passed them on to two Icelandic juveniles that had never been in contact with the southern resident whale. Ford (1991) also showed that on rare occasions groups in the wild mimic calls of other acoustic clans that are not part of their acoustic repertoire. In a preliminary study, Bowles *et al.* (1988) recorded the vocal development of a killer whale calf born in captivity, and found evidence of copying as early as 12 days of age. Deecke *et al.* (2000) examined structural changes in call types shared by two matrilines of northern resident killer whales over a period of 13 years. They found that the call structure changed in both groups, but that the changes paralleled each other. This suggests that structural similarity of discrete calls is maintained through vocal learning and matching.

The precise functions of killer whale vocal communication in general, and of killer whale group dialects in particular, are far from understood. Pulsed calls are long-range signals that can be heard over distances of up to 25 km (Miller 2000a). Ford (1991) argues that killer whale calls function in the maintenance of group cohesion and in coordination of group activity. Most pulsed calls have high and low frequency components that are attenuated differentially. A listening whale therefore can obtain precise information on its distance from a caller, regardless of overall source level. Additionally, the upper frequency component is focussed by the melon and therefore highly directional (Schevill & Watkins 1966; Miller 2000b). For this reason, the relative strength of the upper frequency component communicates the orientation of a calling whale. Having group-specific dialects could serve to make this communication more effective, especially in situations where multiple matrilines associate and acoustic interference is a problem (Ford 1991). Recently, Barrett-Lennard (2000) has shown that repertoire similarity in resident populations is correlated with maternal relatedness and that resident killer whales show negative assortative mating by vocal dialect. This suggests that repertoire variation could play a role in inbreeding avoidance.

5 Objectives of the Current Study

The dietary specialisation of killer whales in the northeastern Pacific presents a fascinating situation. Different populations of animals live in the same habitat, and are very similar if not identical in their morphology, their physiology of sound reception and production, their energetic requirements and their ability to cover large distances on a daily basis. At the same time and probably largely because of their dietary specialisation, some populations show striking differences in their behavioural ecology, social organisation, and population genetics. Because resident killer whales largely feed on salmon, a prey with very poor underwater hearing capabilities (Hawkins & Johnstone 1978), their cost of vocal behaviour is largely an energetic one. Transients, on the other hand, feed on animals with excellent underwater hearing and probably rely on stealth to overcome their prey (Barrett-Lennard *et al.* 1996). This could add a substantial ecological cost for vocal behaviour to an energetic cost that is probably close to identical to that of residents. The occurrence in the same acoustic habitat of two different ecotypes of a predator that relies primarily on acoustic signals for intraspecific communication therefore provides a fascinating and rare opportunity to determine the role of ecological costs, but also of differences in social structure and genetic diversity in shaping acoustic communication systems of animals.

Determining behavioural repertoires of animals and comparing such repertoires between individuals, social groups, populations and species, requires a method that allows division of behaviour patterns into discrete categories. Historically, such categorisation was usually done subjectively by researchers. While such categorisation by humans is often biologically meaningful and able to detect existing categories delineated by the behavioural context, an automated categorisation system that establishes behaviour categories in an objective and repeatable fashion is highly desirable. Such a system is especially valuable in situations where the size of behaviour repertoires is to be established and compared between studies, since different human observers often disagree strongly on the appropriate fineness of categorisation and hence the appropriate size of behavioural repertoires. In Chapter II, I present and test an automated system for the categorisation of vocal patterns from frequency contours that is based on an ART2 neural network (*e.g.*, Carpenter & Grossberg 1987). By calculating similarity of acoustic patterns using dynamic time-warping (*e.g.*, Itakura 1975; Buck & Tyack 1993) and relative rather than absolute frequency differences, this system attempts to circumvent some of the shortcomings of previous methods of automated categorisation.

In Chapter III, I present an analysis of the behavioural context and the frequency of occurrence of vocal activity in mammal-eating killer whales from the northeastern Pacific. I determine during which behavioural states vocal activity is recorded most frequently, and test if vocal activity is associated with the presence of food, that is, whether it occurs more commonly after a successful attack on a marine mammal. I compare these findings with the behavioural context of vocal activity in resident killer whales from the published literature. Finally, I compare the frequency of occurrence of vocal behaviour in resident and transient killer whales to test whether mammal-eating killer whales produce pulsed calls less frequently than members of fish-eating populations, as their higher ecological cost of vocal behaviour predicts.

The analyses in Chapter IV present a shift in perspective - from the aspect of the predator to that of the prey. In the first of two sets of playback experiments, I test whether harbour seals, a common prey of transient killer whales in the coastal waters of British Columbia, respond to the calls of their main predator with evasive behaviour. This question must be answered before one can conclude that transient killer whales pay an ecological cost for vocal behaviour. From the perspective of harbour seals, the vocal differences between resident and transient killer whales provide an interesting challenge: two populations of potential predators with calls that are very similar in their physical properties, yet very different in the amount of danger they signal. In the second set of playback experiments I therefore set out to determine whether harbour seals are able to discriminate between the calls of harmless residents and dangerous transients. In order to determine the role of experience and learning in generating any difference in response, I also test the seals' reaction to calls of Alaskan residents - harmless but unfamiliar killer whales.

While much research has investigated differences in the vocal repertoires within populations of resident killer whales (*e.g.*, Ford 1989; Ford 1991; Deecke *et al.* 2000; Yurk *et al.* 2002), comparatively little is known about vocal variation among transient killer whales. In Chapter V, the final Results chapter, I therefore use the methodology described in Chapter II to categorise calls from 66 recordings spanning the years from 1970 to 2002 and the entire range of the West Coast transient population from California to Southeast Alaska. I analyse variation in the vocal repertoires of different social groups, as well as different parts of the transient range and compare them to those found among resident populations. I discuss differences in the amount of vocal variation found in the two ecotypes of Northeastern Pacific killer whales in the light of differences in their social organisation and amount of genetic diversity.

In summary, the aim of this study is to complement our extensive knowledge about the vocal behaviour of fish-eating populations of killer whales, with information from their mammal-eating counterparts to identify differences the vocal behaviour of these two types of killer whale. The study investigates vocal communication at two separate levels: the timing, context and frequency of occurrence of vocal activity are described in Chapter III, whereas Chapter V looks at the structure of vocal signals and its variation. In Chapter II, I test the methodology necessary for quantifying such structural variation, while in Chapter IV I test an hypothesis that is central to the interpretation of the timing, context and frequency of occurrence of vocal activity in mammal-eating killer whales (and by extension many other predators of acoustically sensitive prey). By comparing the context and nature of vocal behaviour between populations of animals that are nearly identical in many aspects of their biology, yet differ strikingly in a few, I hope to shed light on some of the factors that exert influences on the timing and structure of vocal signals, and thus create variation in vocal communication within and between species of animals.

CHAPTER II - Avoiding Pitfalls in the Automated Categorisation of Behaviour - A Lesson from Bioacoustics

1 INTRODUCTION

1.1 Categorisation of Behaviour by Humans and Computers

A widespread problem in the study of animal behaviour lies in dividing the patterns that make up the behavioural repertoire of a species into biologically relevant categories. Such categorisation is fundamental to any study attempting to compare behavioural repertoires between contexts, individuals, populations or species. Historically, such categorisation was usually carried out by human observers who sorted the behaviour patterns into categories according to their perceived similarity. Categorisation by human observers has an inherent subjectivity since it requires the observer to decide which features are important in defining categories and how these features should be weighted. This subjectivity can be hard to quantify, which often makes it difficult to compare behavioural repertoires between different studies. In addition, categorisation can often be a time-consuming process thus limiting the amount of data included in any comparison. To overcome the problems of observer subjectivity and time constraints, researchers have, with varying degrees of success, turned to automated methods of categorisation. These have included clustering schemes based on various measures of similarity (e.g., Symmes *et al.* 1979; Chabot 1988; Burns *et al.* 1997), principal components analyses (*e.g.*, Clark 1982; Cerchio & Dahlheim 2001), or combinations of these procedures (e.g., Elowson & Hailman 1991; McCowan 1995; Schreer & Testa 1996; Lesage *et al.* 1999; Krafft *et al.* 2000).

For many problems of categorisation in the field of acoustics, studies have confirmed that human observers do perceive similarity of sound patterns in a way that is biologically meaningful (e.g., Deecke *et al.* 1999), and are able to detect biologically relevant behaviour categories (e.g., Janik 1999). However, observer subjectivity and the resulting inability to replicate and compare results between studies continue to be a problem. Jones *et al.* (2001) have recently shown that observers classifying acoustic patterns from spectrograms do not always arrive at the same biological conclusions, and that classifications are to a high degree influenced by the experience of the observer. In some cases, these problems can be overcome by replicating the categorisation with a large number of observers, but this is usually logistically impractical. In many situations, therefore, an automated method that categorises acoustic behaviour in a biologically meaningful way would be a valuable analytical tool for the study of animal behaviour.

Particularly in the field of bioacoustics, currently available methods of automated categorisation leave much to be desired. Standard methods often fall far short of observer ratings in accuracy, and frequently fail to detect biologically meaningful categories (see Janik 1999). I argue here that this poor performance is largely due to the failure of most methods to take into account two fundamentals of acoustic perception when measuring the similarity of sound patterns. I also suggest that researchers on vocal behaviour can benefit a lot from recent advances in the study of human perception and speech recognition (so long as the peculiarities of the human communication system are kept in mind).

1.2 Time and Frequency Resolution in the Auditory Perception of Birds and Mammals

One shortcoming of any study using frequency contours (plots of the fundamental frequency of a vocalisation over time) is that in order to compare two contours using most standard distance measures, they need to be standardised for time. This can have the effect of rating two sound patterns as very similar even though their lengths might differ by an order of magnitude. In addition, for signals with strong frequency modulation, temporal standardisation can have the effect of generating artificially low similarity values for signals that are in fact very similar in shape, but instead differ only slightly in the length of different components so that equivalent sections of the signals do not overlap (see Figure 1). An important point to bear in mind in the automated categorisation of sounds is that animals are relatively insensitive to slight differences in the duration of sound patterns. Dooling (1982) suggests that birds are 10 times more sensitive to changes in the frequency of sounds than they are to changes in their duration. Small differences in the duration of certain acoustic features are therefore often insignificant to the animal and any automated analysis of sound patterns must accommodate this.

Another feature of vertebrate auditory perception that needs to be considered when developing automated methods of acoustic categorisation is that tonal frequency is not perceived on a linear but on an exponential scale. Humans perceive the difference between two tones with frequencies that differ by a factor of two (an octave) as being the same regardless of whether the two tones have frequencies of 110 Hz and 220 Hz or 880 Hz and 1760 Hz. This exponential perception of frequency is reflected by the distribution of hair cells sensitive to different frequencies in the inner ear and appears to be common to all terrestrial vertebrates (*e.g.*, Müller 1991; Smolders *et al.* 1995; Vater & Siefer 1995; Manley *et al.* 1999). This means that acoustic features with higher fundamental frequencies can exhibit greater absolute frequency variation before they are perceived as different compared to features with low fundamental frequencies. Frequency measurements should therefore be log-transformed before comparison, or differences in frequencies should be expressed as relative rather than absolute values. Any scheme that fails to account for the exponential perception of frequency runs the risk of biassing categorisation towards an inflated number of categories of high-frequency sound patterns.

1.3 Unsupervised Learning in Artificial Neural Networks

Supervised and unsupervised learning describe two different applications of self-organising artificial neural networks. In supervised learning, an artificial neural network learns to classify unknown patterns using information extracted from a training set of identified patterns. For example, artificial neural networks can be trained in this way to distinguish between the vocal patterns of different identified individuals (*e.g.*, Reby *et al.* 1997; Campbell *et al.* 2002; Terry & McGregor 2002), social groups (e.g., Deecke *et al.* 1999), or species (*e.g.*, Phelps & Ryan 1998; Parsons & Jones 2000), or between vocal patterns given in response to clearly identifiable stimuli (e.g., predator-specific calls; Placer & Slobodchikoff 2000). In contrast, unsupervised learning describes a series of artificial neural network algorithms that can be used to categorise patterns without prior training. The most common algorithms for unsupervised learning are self-organising maps (SOM, *e.g.*, Kohonen 1988), competitive learning (*e.g.*, Grossberg 1987) and adaptive resonance theory (ART) neural networks (*e.g.*, Carpenter & Grossberg 1987). Unsupervised learning algorithms are self-organising analogs of traditional clustering schemes. Their main advantage is that, for a new pattern to be assigned to a category, it must only be compared to a small subset of reference patterns (or neighbouring patterns in the case of self-organising maps) rather than all other inputs in the data set. Unsupervised learning algorithms therefore lend themselves to the analysis of large data sets where computing time is limiting, or to situations where categorisation must happen in real time.

Unsupervised learning algorithms have been used in the past for the categorisation of behavioural data. Leinonen *et al.* (1993) used a self-organising map to classify consonants followed by different vowels and found that the results agreed with perceptual classifications. Terry & McGregor (2002) tested the usefulness of self-organising maps to determine the number of corncrakes (*Crex crex*) in a population from recordings of their individually distinctive calls and showed that population estimates were correct to within one individual for data sets containing the calls of up to 16 individuals. Schreer *et al.* (1998) tested the performance of a self-organising map and ART neural network at categorising dive-trajectories of penguins and pinnipeds but found that the neural networks did not perform better than traditional statistical clustering methods.

1.4 Objectives

In this chapter, I present and test an automated method designed to categorise stereotyped vocal patterns based on an ART2 neural network. ART2 is an unsupervised learning algorithm in which a certain input pattern is compared to a set of reference patterns. If the input pattern resembles one of the reference patterns with a certain degree of similarity (called the vigilance), the input is assigned to the category represented by this reference pattern and the reference pattern itself is updated and made even more similar to the input pattern. If the input pattern does not resemble any reference pattern sufficiently, it becomes the reference pattern for a new category. ART2 neural networks have the advantage that they do not require assumptions about the frequencies of patterns in different categories. In contrast, competitive learning algorithms and self-organising maps assume that input patterns are evenly distributed between categories and therefore tend to split frequent input patterns into finer categories. ART neural networks therefore lend themselves to the categorisation of behaviour patterns where equal distribution can rarely be assumed.

In order to allow for temporal imprecision in the lengths of different components of the patterns, similarities between input and reference patterns were calculated using dynamic time-warping (*e.g.*, Itakura 1975). Dynamic time-warping is an algorithm developed for the automated recognition of human speech that allows limited modification of the time axis of a signal to maximise frequency overlap with a reference signal (see Figure 1 for an illustration of dynamic time-warping).

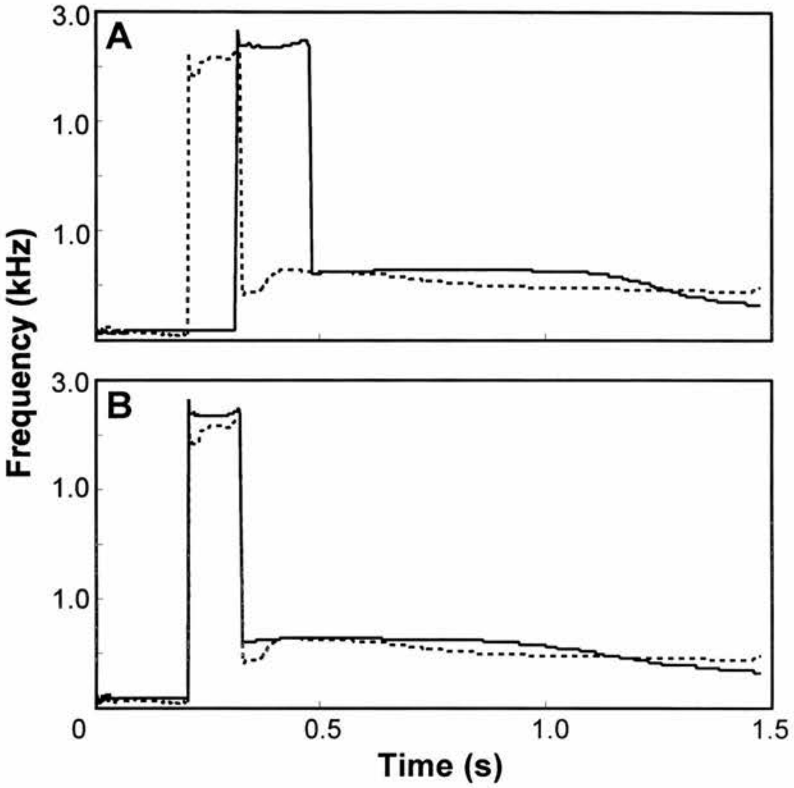


Figure 1: Matching a frequency contour of a pulsed call of transient killer whales (solid line) to a reference contour (dotted line) using standardisation of call length (panel A) and dynamic time warping (panel B). The match (given as the average similarity in frequency in percent for all points of the two contours) is 69.9% using standardisation, but 86.9% using dynamic time warping.

Dynamic time-warping has been used successfully to improve the automated classification of bottlenose dolphin (*Tursiops truncatus*) whistles from frequency contours (Buck & Tyack 1993). To account for exponential perception of frequency in this analysis, I expressed similarity of contours as their relative similarity in frequency.

I test the performance of this method on two categorisation problems. The first is a set of frequency contours of bottlenose dolphin whistles described in detail by Janik (1999). The sample consists of 104 randomly chosen whistles from four captive bottlenose dolphins and includes distinctive stereotyped whistles made when each individual was kept in isolation. The data set therefore contains at least four naturally defined categories and can be used to test the performance of categorisation methods in detecting these.

In many situations, it is desirable to explain the maximum of behavioural variation using the minimum number of categories. In ART neural networks, the vigilance parameter controls the fineness of categorisation and therefore the number of categories established. Using a set of frequency contours of calls of transient killer whales, the second problem serves to illustrate how the optimal vigilance parameter (which minimises variation within categories while maximising differences between categories) can be determined in a simple experiment. Finally, using a small enough set of frequency contours that can be plotted on a single page, I illustrate how the described method categorises the calls of transient killer whales.

2 METHODS

2.1 Acoustic Analysis and Contour Extraction

Both the dolphin whistle and killer whale call data sets consisted of frequency contours extracted from spectrograms of calls or whistles. Dolphin whistles are tonal signals and frequency contours therefore give the fundamental frequency of a whistle as a function of time. The time resolution for the extraction of frequency contours for the dolphin whistles was 10 ms. For details on the selection of bottlenose dolphin whistles and extraction of frequency contours see Janik *et al.* (1994) and Janik (1999).

The frequency contours of killer whale calls were generated from a sample of calls derived from 25 field recordings of transient killer whales. I rated the quality of each call from the spectrogram on a scale from one to five, taking in to account signal-to-noise ratio, echoes and reverberation, and background noise. In order to avoid categorisation due to noise artefacts (*e.g.*, faint call elements that were missed), only calls of the two highest quality categories were included in this analysis. Since killer whale calls are pulsed signals (Schevill & Watkins 1966), frequency contours give the pulse-repetition rate rather than fundamental frequency. I used the sidewinder algorithm (Deecke *et al.* 1999) to extract frequency contours from spectrograms of killer whale calls, with the difference that for the current analysis the contours were not standardised for time. Time resolution for the frequency contours was also 10 ms.

2.2 ARTwarp - Combining Dynamic Time-warping and Adaptive Resonance Theory

The neural network used in this analysis was an ART2 neural network for the categorisation of analog input patterns. The computer script was a simulation of the ART2 algorithm of Carpenter & Grossberg (1987). However, this algorithm was modified in two ways. First the similarity between frequency contours and the set of reference contours was calculated using dynamic time-warping to ensure maximum overlap in the frequency domain. If a frequency contour matched a reference contour better than the critical similarity (vigilance), this reference contour was then modified in three ways to be more similar to the input pattern. 1) The frequency content of the reference contour was made more similar to the time-warped frequency contour. 2) The relative lengths of different components of the reference contour were modified to be more similar to the current frequency contour by applying the inverse of the warping function. 3) The length of the reference contour was made more similar to the current frequency contour. If the current input pattern did not match any of the reference patterns better than the critical similarity, it became the reference contour for a new category. All frequency contours were repeatedly presented to the neural network until they consistently matched the same reference contour (*i.e.* no reclassifications occurred between iterations).

The dynamic time-warping algorithm used in this study was that applied by Itakura (1975) and Buck & Tyack (1993) with the difference that the algorithm allowed horizontal and vertical jumps of three elements in the contour (rather than two elements as in Itakura,1975, and Buck & Tyack, 1993). A frequency contour can therefore be 'sped up' or 'slowed down' in parts by a factor of three to fit the reference contour. In addition, the algorithm calculated the relative frequency similarity (*S*) in percent between both frequency contours rather than the total square difference as in Itakura (1975) or the average square difference of Buck & Tyack (1993). This was done by dividing the smaller frequency value by the larger value at each point and multiplying by 100:

$$S(i) = \frac{\min[M(i), N(i)]}{\max[M(i), N(i)]} * 100$$

where *M* is the reference pattern, and *N* the input pattern. Like Buck & Tyack (1993), I also divided the total difference by the length of the reference contour and the measure of similarity therefore gives the average relative similarity in frequency for the reference and input contour after time warping.

2.3 Experiment I: Categorisation of Bottlenose Dolphin Whistles

The level of critical similarity for the analysis of dolphin whistles was obtained by categorising only the signature whistles of one individual (individual A of Janik, 1999) and increasing the vigilance in steps of 1% until the analysis split these signature whistles into two categories. The critical vigilance (96%) is the highest value that still recognises the whistles as a single category. The entire data set was then categorised using this vigilance parameter and the resulting categories were analysed to test whether the signature whistle categories were recognised.

2.4 Experiment II: The Appropriate Fineness of Categorisation

In this experiment, I categorised a sample of 50 frequency contours randomly selected from my data set of transient killer whale calls. Initially the vigilance was set at zero. At this level, call categories are assigned only by call length (since any two contours whose length differs by more than a factor of three are automatically assigned a similarity of zero; see Buck & Tyack, 1993). The vigilance was then increased to 100% in 50 logarithmic steps and the sample was categorised. At a vigilance of 100%, each frequency contour is assigned to its own category. For each categorisation, I determined the number of categories generated, as well as the average fit (the average level of similarity for each frequency contour and its most similar reference contour), as an estimate of the within-category variation. In order to estimate the between-category variation, I calculated the average similarity (using dynamic time-warping) between the reference contours of all categories. The categorisation where a minimum number of distinct categories explain a maximum amount of difference in the frequency contours can then be identified by plotting the ratio of variation within categories and variation between categories and determining the vigilance that corresponds to the maximum ratio.

2.5 Experiment III: Visualisation of Neural Network Performance

In order to illustrate how the ARTwarp algorithm categorises the discrete calls of killer whales from frequency contours, I used the neural network to categorise a sample of 20 frequency contours that could be graphed on a single page. These were randomly chosen from the two highest quality categories in the data set of transient killer whale calls. The vigilance parameter used in this analysis was the value that yielded a maximum ratio of within- to between-category variation in Experiment II.

3 RESULTS

3.1 Experiment I: Categorisation of Bottlenose Dolphin Whistles

The categorisation of the data set of bottlenose dolphin whistles is shown in Figure 2. Using a vigilance of 96%, the analysis divided the 104 whistle contours into 46 categories each containing between one and 14 contours (mean: 2.26, standard deviation: 2.62 contours).With regard to the behaviourally defined categories of signature whistles recorded from each of the five dolphins in isolation, the analysis correctly detected two whistle types (A and D_2) but made three errors while categorising the other three whistle types: It added an additional whistle (no. 75) to the category containing the contours of whistle type C. In the case of whistles types B and D_1, a single contour was not assigned to the category containing the whistle types, but was put in a category of its own.

3.2 Experiment II: The Appropriate Fineness of Categorisation

The effects of increasing the vigilance parameter on the categorisation of transient killer whale calls are illustrated in Figure 3. With higher vigilance the analysis generated an increasing number of categories. Both the distance of frequency contours to their nearest reference contour (with-category variation) and the average distance of the reference contours to each other (between category variation) decreased as the number of categories increased, but they did so at differential rates. Initially the rate of decrease in the between-category variation was relatively low and the rate of decrease in the within category variation was high. At a critical point, however, the rate of decrease in the within category variation slowed (since new categories explain little additional variation) and the rate of decrease in the between-category variation increased (since more and more natural clusters in the data set were divided between categories). The plot of the F-ratio of within and between-category variation (Figure 3) therefore showed a peak at a vigilance of 81.24%. At this point the analysis generated 10 categories.

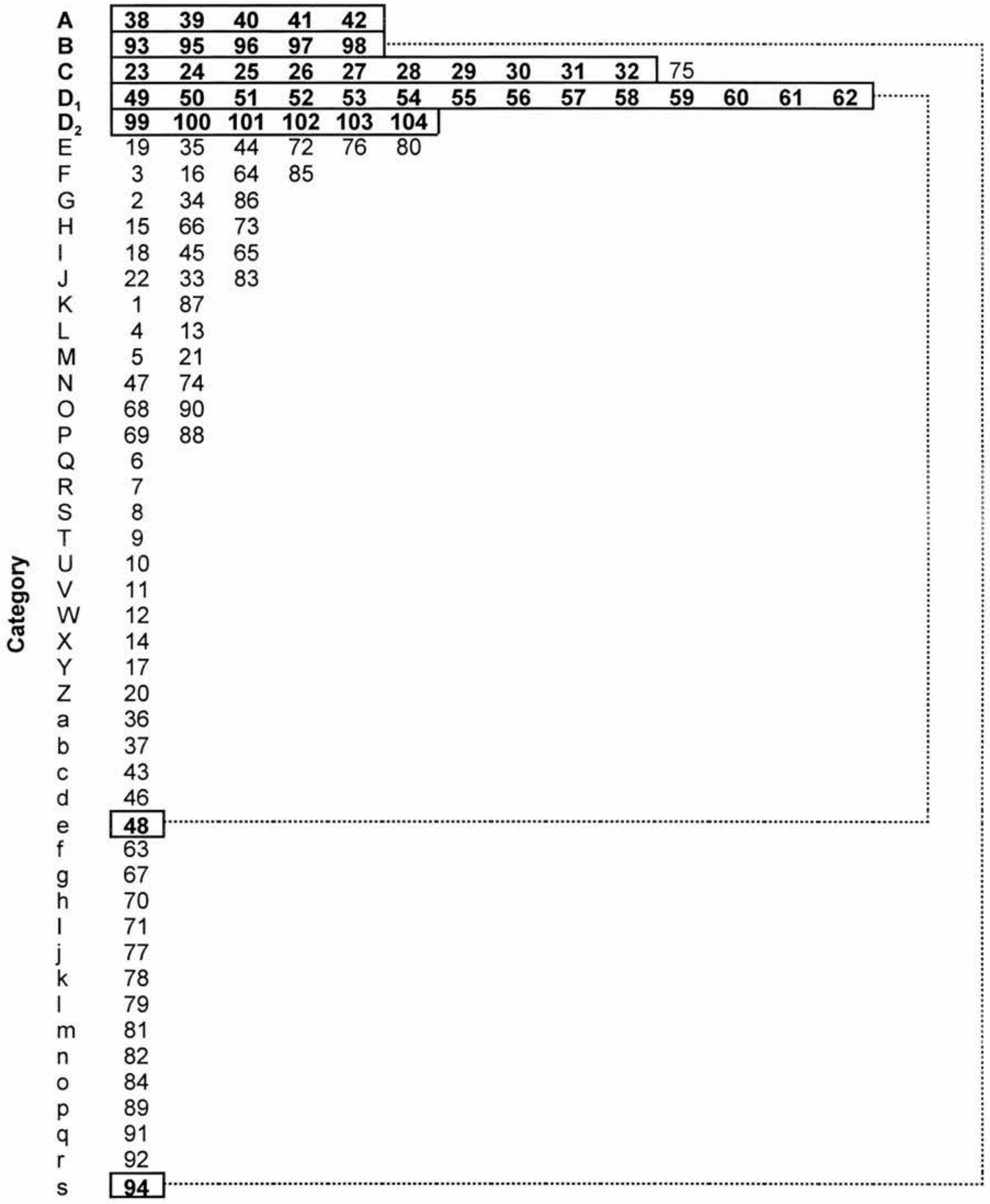


Figure 2: Categorisation of frequency contours of bottlenose dolphin whistles using an ART2 neural network and dynamic time warping to calculate similarity. Numbers represent individual whistle contours. Signature whistles are shown in bold and boxes identify signature whistles from the same individual. Signature whistle categories that were split by the analysis are linked with dotted lines. Contours and signature whistle categories are labeled consistent with Janik (1999).

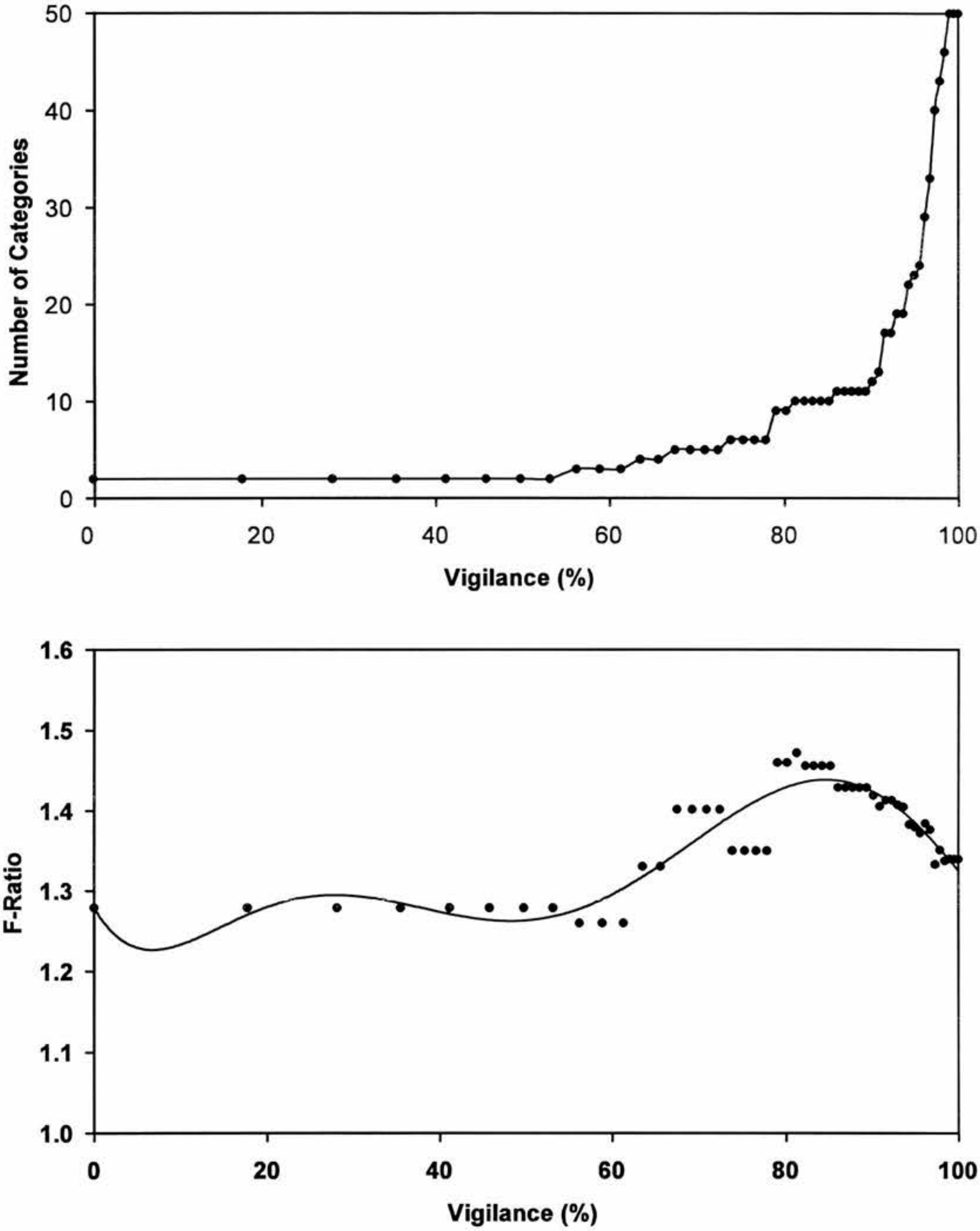


Figure 3: Effect of the vigilance on the categorisation of 50 frequency contours from calls of transient killer whales. Panel A shows the increase in the number of categories generated with increasing vigilance. Panel B shows the change in the ratio of within- to between-category variation with increasing vigilance. This ratio reached a maximum at a vigilance of 81.24% (10 categories). The trend line is a 6th order polynomial.

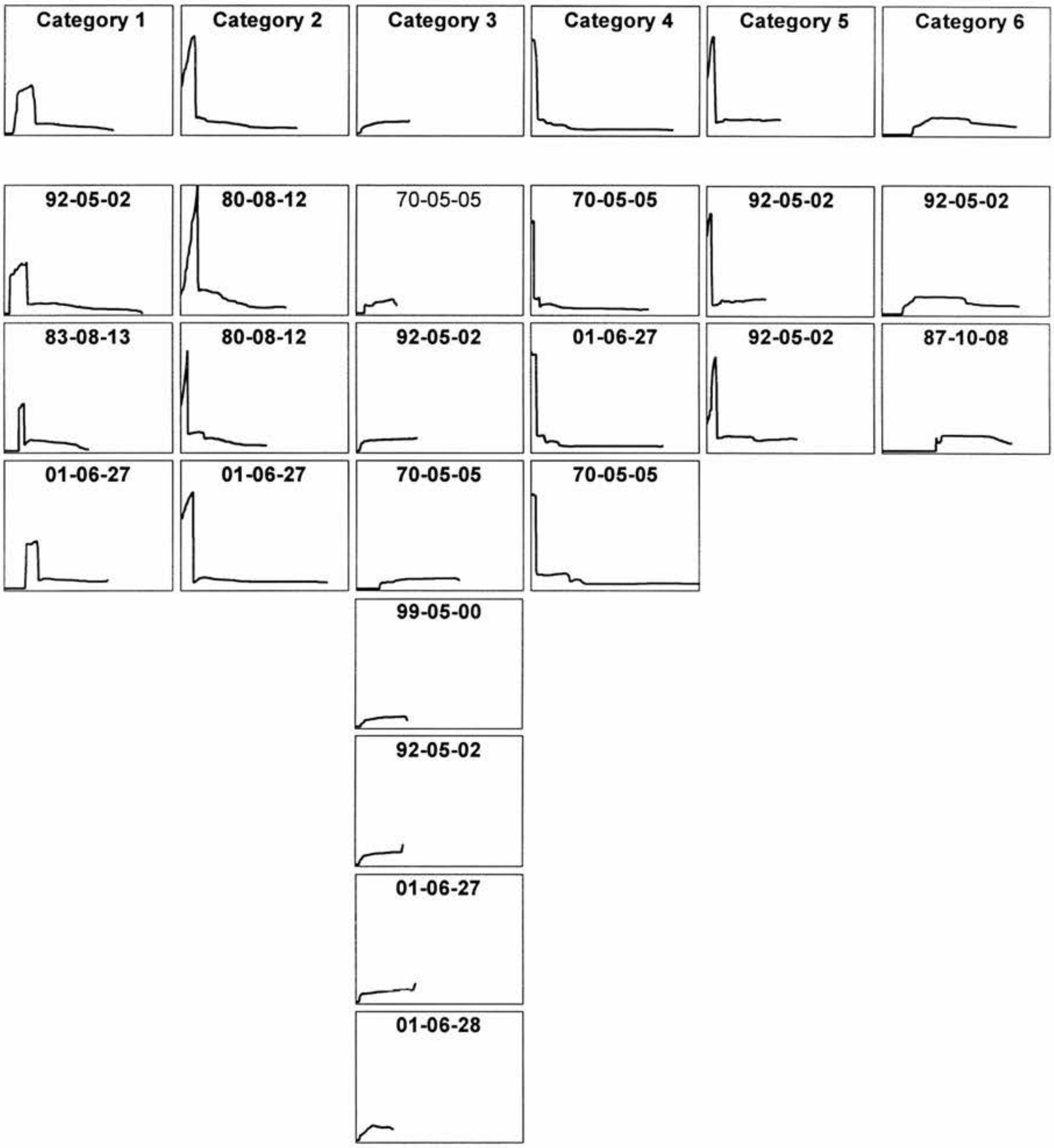


Figure 4: Results of the categorisation of frequency contours from 20 randomly chosen calls of transient killer whales to illustrate the performance of the categorisation algorithm. All frequency contours in the same column were assigned to the same call type by the analysis. The reference contours representing each category are shown in the first row. Labels give the recording session (in the format yy-mm-dd) of each frequency contour.

3.3 Experiment III: Visualisation of Neural Network Performance

The frequency contours used in this experiment, as well as the resulting call categories are shown in Figure 4. The analysis divided the 20 contours into six categories each containing between two and seven calls. The categories were largely consistent with the call types established by Ford & Morton (1991): Category 1 contained calls classified as T08i, Category 2 represents the T04 call type of Ford (1984) and the T03ii call type of Ford & Morton (1991), Category 3 is equivalent to the T01 call type, and Category 4 represents the T07 call type of Ford & Morton (1991). Category 5 contained calls classified as subtype T07ii by Ford & Morton (1991), and Category 6 is equivalent to their T02 call type.

4 DISCUSSION

4.1 Categorisation of Bottlenose Dolphin Whistles

The automated categorisation combining dynamic time-warping with an ART2 neural network performed marginally better at detecting the biologically defined behaviour categories in the data set of bottlenose dolphin whistles than did the human observers of Janik (1999) who made an average of 3.4 mistakes. It performed much better than any of the statistical procedures tested by Janik (1999). Interestingly, the neural network did not agree with the human observers in the categorisation of non-signature whistles. In general, the automated analysis created finer categories containing fewer contours for this subset. Janik (1999) identified four combinations of non-signature whistles common to the categorisation of all five observers and none of these combinations occur in the neural network categorisation. Since we have no external validation for appropriate classification of non-signature whistles it is impossible to say which categorisation scheme is of greater biological relevance.

The two signature whistles that were assigned to separate categories from the rest of their whistle types are both shorter than the other whistles of the same type and may represent truncated versions of the individuals' signature whistles. If this is the case, relaxing the endpoint constraint during dynamic time-warping (*i.e.* permitting the time-warped contour to be shorter in duration than the reference contour and calculating frequency similarity only for the section of overlap with the reference contour; see Parsons, 1987) would improve classification for these contours.

4.2 Choosing the Vigilance Parameter

Most automated analytic procedures require the investigator to choose some parameters that control their performance. In the automated categorisation described here, the performance depends to a large degree on the vigilance of the neural network. This parameter controls the fineness of categorisation, that is, the size and number of categories that are generated. It has no influence on which patterns are rated as similar in the analysis. Note that the problem of deciding on the appropriate fineness of categorisation is shared by categorisation of behaviour using human observers: we refer to observers as 'joiners' or 'splitters' depending on how fine their behaviour categories tend to be. As an example, Saulitis (1993) divides the surface behaviour of killer whales into 14 categories, whereas (Ford 1989) distinguishes between only five behaviour categories. We have no information on the extent to which this difference is due to differences in the behaviour of killer whale populations studied by the two researchers, or differences in the fineness of categorisation considered appropriate to describe the observed behavioural variation by the authors . The advantage of the automated procedure is obviously that the fineness of categorisation can be quantified for each analysis.

As demonstrated in the categorisation of bottlenose dolphin whistles where biologically relevant behaviour categories can be identified, these can be used to determine the vigilance parameter appropriate for categorisation. Such biologically defined behaviour categories may be behaviour patterns specific to certain individuals or populations or to clearly defined contexts (such as isolation from group members in Symmes *et al.* 1979, and Janik 1999, or the presence of a food source in Judd & Sherman 1996, and Roush & Snowdon 2000). Human observers frequently use such information from predefined categories (although not always consciously) to determine the appropriate resolution for behavioural categorisation.

In many studies of animal behaviour, it is desirable to explain a maximum amount of the observed behavioural variation using a minimum number of behaviour categories. In situations where behaviour variation is difficult to quantify, this can be hard to achieve. However, wherever measures of behavioural similarity are readily available, simple algorithms can help to determine the appropriate number of categories for analysis. In situations where no external validation of categories is available, calculating the ratio of variation within to variation between categories for a large number of vigilance values provides a useful approach to determining the appropriate fineness of categorisation. This is time-consuming for large samples of behaviour patterns but, as demonstrated in Experiment II, categorisation of a randomly selected subset will generally allow identification of the appropriate vigilance parameter.

4.3 Applicability to Other Categorisation Problems in the Study of Behaviour

While this method of automated categorisation has so far only been tested on cetacean vocalisations, these results should also encourage its application to analyses of vocal behaviour in other species. As described here, the analysis is limited to species whose vocalisations can be described adequately by frequency contours. This includes many amphibians, birds and mammals. However, in species with vocalisations that are broadband (*e.g.*, Campbell *et al.* 2002), or where relevant information is encoded in the harmonic content (*e.g.*, Weiss & Hauser 2002), frequency contours alone are inadequate to describe vocal patterns. Fortunately, dynamic time-warping can also be used to compare spectrograms (it was in fact first developed to classify human speech patterns from spectrograms, see Itakura 1975) and the neural network component of the analysis could easily be adapted to deal with the two-dimensional format of spectrograms rather than one-dimensional frequency contours, making the analysis applicable to the categorisation of vocal behaviour in a wide-variety of species.

Since it was developed to address peculiarities of acoustic perception, the methodology as described in this study is probably of limited value to categorise behaviours other than those that are acoustic. Nonetheless, elements applied in the current analysis may prove useful elsewhere: dynamic time-warping and its extension of hidden Markov models will be useful in any situation where the trajectory of change in a behavioural parameter is more important than the precise timing of the change. The categorisation of dive profiles from aquatic birds and mammals (*e.g.*, Schreer *et al.* 1998; Lesage *et al.* 1999; Malcolm & Duffus 2000) may prove to be a valuable example. In addition, much if not most of sensory perception is non-linear in scale (usually exponential or logarithmic), and this is important to bear in mind when quantifying the strength and quality of behavioural stimuli for categorisation. This study therefore serves to illustrate the importance of obtaining and applying relevant information about the sensory perception of study animals when designing categorisation schemes for the study of their behaviour.

CHAPTER III - The Context of Vocal Behaviour in Transient Killer Whales - Food Calling or Constrained Communication?

1 INTRODUCTION

1.1 Constraints on the Vocal Behaviour of Predators

Vocal behaviour in mammals and birds has two principal functions. First, vocalisations are used in communication to transmit information between individuals and so influence the behaviour of other animals (Slater 1999). Second, in a few groups of animals living in environments where vision is limited, vocal behaviour in the form of echolocation is used for orientation in the environment and for prey detection (*e.g.*, toothed whales: Norris *et al.* 1961; Au 1993; bats: Novick 1977; Møhl 1988; birds: Griffin & Thompson 1982). While vocal behaviour clearly generates benefits in both situations, it also has associated costs: in addition to the energy required to generate the sound signals, vocalising animals may experience costs from passing on information to unintended receivers. In the case of predators that specialise on prey with sensitive hearing, these costs can be substantial, since the prey is likely to react to the predator's vocalisation thus greatly reducing the predator's probability hunting success.

The coevolution between the vocal behaviour of predators and the hearing ability of their prey has been studied extensively in insectivorous bats *(e.g.*, Fenton

& Fullard 1981; Rydell *et al.* 1995). Most insectivorous bats rely entirely on echolocation for prey detection making vocal behaviour obligatory during foraging. While many insects are deaf to the echolocation signals of bats, others, such as tympanate moths (Lepidoptera) or lacewings (Neuroptera) have evolved sensitive hearing at the frequencies of bat echolocation (Roeder 1967), and studies have shown that these insects are taken less frequently by most bats (Fenton & Fullard 1981; Fullard 2001). In turn, some species of bats have evolved echolocation signals with frequencies outside the range of best hearing of tympanate moths and lacewings, and are therefore able to specialise on these insects (Rydell & Arlettaz 1994; Rydell *et al.* 1995; Fullard & Dawson 1997; Pavey & Burwell 1998).

Predatory animals that hunt acoustically sensitive prey and use vocal behaviour for communication but not for prey detection would be expected to reduce vocal behaviour while hunting to avoid being detected by their prey. This can be achieved either by reducing communication altogether or by shifting the transfer of information to a sensory channel not received by the prey. Evidence for this behavioural strategy comes from chimpanzees (*Pan troglodytes*) when hunting small forest monkeys: in most behavioural contexts, chimpanzees in the Taï forest frequently maintain contact using a variety of acoustic signals. However, acoustic communication usually ceases completely when members of a group have detected the calls of their intended prey and started to hunt (Boesch & Boesch 1989; Boesch & Boesch-Achermann 2000).

Vocal behaviour has therefore been shown to differ between species of bats and between behavioural contexts in chimpanzees to avoid detection by the prey. Few studies have investigated differences in the vocal behaviour between populations of the same species that differ in their prey spectrum. In the Northeastern Pacific, two distinct ecotypes of killer whale (*Orcinus orca)* specialise on different prey: resident killer whales live in large stable groups and feed exclusively on fish, preferentially on chinook salmon (*Oncorhynchus tshawytscha*). Transients, on the other hand, hunt marine mammals including harbour seals (*Phoca vitulina*), Steller and California sea lions (*Eumetopias jubatus* and *Zalophus californianus*), harbour porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli*), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), and occasionally take seabirds (Ford *et al.* 1998; Saulitis *et al.* 2000). Resident and transient killer whales do not interbreed and rarely interact (Barrett-Lennard 2000) despite the large degree of overlap of their home ranges (Ford & Ellis 1999; Matkin *et al.* 1999; Ford *et al.* 2000). While the fish eaten by resident killer whales are essentially deaf to the frequencies of killer whale vocalisations (Hawkins & Johnstone 1978), many marine mammals taken by transient killer whales have excellent underwater hearing (*e.g.*, Renouf 1992; Au *et al.* 2000; Kastelein *et al.* 2002; Wolski *et al.* 2003). Hence it seems likely that transient killer whales pay a greater ecological cost than residents for vocal behaviour.

1.2 Food-related Vocal Behaviour in Birds and Mammals

Vocal behaviour in the context of the discovery or manipulation of food has been described in a variety of birds and mammals. Eusocial naked mole-rats (*Heterocephalus glaber*) inform colony members of their discovery of a food source using a behavioural display that includes specific vocalisations (Judd & Sherman 1996). Since colony mates are closely related, food-related signalling benefits close kin and increases the inclusive fitness of the signaller. Many species of group-living birds and mammals similarly emit specific vocalisations upon discovery of a divisible food source (*e.g.*, Dittus 1984; Elgar 1986; Chapman & Lefebvre 1990; Bugnyar *et al.* 2001), and conspecifics usually respond by approaching the caller. In these cases, food calling could also benefit kin (*e.g.*, Hauser & Marler 1993), or, by attracting conspecifics, could decrease the risk of predation for the signaller (*e.g.*, Elgar 1986; Chapman & Lefebvre 1990), attract potential mates (*e.g.*, Stokes & Williams 1972; Van Krunkelsven *et al.* 1996), or lead to improved access to the food source (*e.g.*, Marzluff & Heinrich 1991). Social foragers may give food calls that transmit information about the quality of a food patch within a group thus optimising time spent on a given patch (Valone 1996).

However, vocal behaviour while foraging or manipulating food does not necessarily need to be directed towards conspecifics. In the case of echolocating bats and cetaceans, the emission of sound is essential for prey detection and thus part of the foraging process. In predatory animals, vocalisations may be used to manipulate the behaviour of the prey: Norris & Møhl (1983) hypothesised that cetaceans may be able to debilitate prey using extremely loud broad-band vocalisations. Research on killer whales, however, suggests that such sounds recorded around feeding cetaceans may not be vocalisations but rather are generated when the animals strike a school with their tail flukes (Domenici *et al.* 2000). Humpback whales (*Megaptera novaeangliae*) feeding on schooling herring in Alaska using bubble nets emit stereotyped underwater vocalisations, which may serve to concentrate the prey (D'Vincent *et al.* 1985; Cerchio & Dahlheim 2001; Sharpe 2001). Janik (2000) documented food-associated vocalisations in bottlenose dolphins (*Tursiops truncatus*) and suggested that their primary function is to manipulate the behaviour of prey. Although vocalisations used to detect or manipulate the behaviour of prey are not directed towards members of the same species, they may still attract conspecifics, since they indicate the presence of prey (Barclay 1982; Janik 2000).

1.3 The Vocal Behaviour of Killer Whales

Killer whales produce three major types of vocalisations: echolocation clicks, whistles and pulsed calls (Ford 1989). Clicks are short pulses of sound, usually emitted in series, and are used in echolocation for orientation and prey detection (Awbrey *et al.* 1982; Barrett-Lennard *et al.* 1996). Whistles are tonal signals with little or no harmonic content and tend to be most common in social contexts (Ford 1989; Thomsen *et al.* 2002). Pulsed calls are the most common vocalisation of killer whales (Ford & Fisher 1982). Due to the high pulse repetition frequencies, these calls have distinct tonal properties. Ford & Fisher (1982) and Ford (1989) grouped pulsed calls into three categories. *Discrete* calls are highly stereotyped and can easily be assigned to different call types according to their structural properties. Ford & Morton (1991) described 7 discrete call types from the West Coast transient population and gave them alphanumeric designations (T01, T02, *etc.*). *Variable* calls are not stereotyped and cannot be divided into clearly defined call types. Finally, *aberrant* calls are structurally based on a discrete call type, but show some degree of modification. Like whistles, aberrant calls tend to occur most frequently during social interactions (Ford 1989).

Barrett-Lennard *et al.* (1996) compared the use of echolocation by resident and transient killer whales and found that transient killer whales emitted far fewer echolocation clicks than residents. In addition, transients either emitted single clicks, or short irregular click trains, which presumably makes their echolocation harder to detect in background noise. Since transient killer whales often travel and forage without echolocating, Barrett-Lennard *et al.* (1996) suggested that transients detect their prey primarily by passive listening. So far no study has investigated differences in the use of communicative vocalisations in the two forms of killer whale.

Guinet (1992) studied the acoustic behaviour of killer whales around the Crozet Islands, where the animals feed predominantly on elephant seals (*Mirounga leonina*) and penguins (*Eudyptes* spp.). He noted that the whales were usually quiet during the hunt, emitting only occasional echolocation clicks and faint calls. Upon detection of an elephant seal in the water, one of the whales would usually emit a single faint call, causing the others to approach. Once a kill had been made, the whales would often start vocalising loudly, and other individuals would approach the site of the kill at great speed, often from distances of several kilometres.

1.4 Objectives

In this study I wanted to combine underwater recording with analysis of the animals' movements and surface activity to investigate the behavioural context of vocal behaviour in mammal-eating killer whales in the coastal waters of the Northeastern Pacific. I predicted that, since the vocal behaviour of transient killer whales potentially carries a high ecological cost in terms of alerting the acoustically sensitive prey, it should occur primarily in situations where this cost is comparatively low. Such situations include the time after a kill of a marine mammal when the animals are satiated and, since kills often involve fast swimming and percussive manipulation of the prey, other potential prey animals in the area may already be aware of the whales' presence. Vocal behaviour could also be common in situations where capture of additional prey is not the best way to promote the fitness of group members, for example, when several groups travel together, which provides opportunities for mating, or when the probability of establishing contact with other groups in the area by vocalising is high. In addition, I wanted to test whether vocal behaviour in transient killer whales is related to the presence of food. If vocalisations are used to signal the presence of food or to manipulate the prey's behaviour, then levels of vocal activity should be elevated during or after a kill compared to other behavioural contexts.

Finally, I wanted to compare how frequently residents and transients vocalise. While the energetic costs of vocalising are probably comparable for fish-eating residents and mammal-eating transients, the additional ecological costs for vocal behaviour are likely to be much greater for transient killer whales. Since residents mainly feed on fish with poor hearing abilities at the frequencies of killer whale calls, their vocal communication is not constrained by the possibility of alerting their prey. Transients, on the other hand, potentially experience a significant additional cost for calling, since prey animals within acoustic range could detect the calls and respond with anti-predator behaviour. Therefore I predicted that across all behaviour categories, transients should vocalise less frequently than residents since this would make them acoustically less conspicuous.

2 METHODS

2.1 Data Collection and Classification of Behaviour

This study was carried out in the summer months (June to October) of 1999-2002 in the waters of Johnstone and Queen Charlotte Straits, British Columbia, and in Glacier Bay and Icy Strait, Southeast Alaska. Groups of transient killer whales were detected by scanning from the boat or from elevated points on shore using binoculars. In addition, opportunistic sightings were often relayed by a network of observers including other researchers, whale-watching operators, recreational boaters and the staff of Glacier Bay National Park Preserve. When a group of killer whales was encountered, the identity and size of the group was confirmed by taking identification photographs of all individuals for comparison with existing catalogues (Ford & Ellis 1999). Encounters are labelled by date in the format yy-mm-dd (*e.g.*, 00-07-01).

To monitor the vocal behaviour of a group, I moved the boat approximately 800 m ahead of the animals but not in their immediate path, so that ideally they would pass the boat at a distance of about 150 m. An Offshore Acoustics hydrophone was used to monitor vocal behaviour, and each time the animals surfaced, their distance from the boat was estimated and confirmed with laser rangefinders (Bushnell YardagePro 1000 or Leica Geovid 7 x 42 BDA) whenever possible. The behaviour of the animals was noted for each such pass, and the position of the boat was determined approximately every 30 min using GPS. The signal from the hydrophone and voice notes, indicating the animals' distance and behaviour, were recorded onto separate channels using a Sony TCD-D8 DAT recorder. In addition, I collected information about attacks on marine mammals. Attacks after which prey remains were clearly seen or could be recovered were noted as *confirmed* kills. If there was only indirect evidence that prey had been captured (seagulls hovering above the whales, crunching sounds on the hydrophone), this was documented as a *possible* kill. Behaviour was divided into categories using variables that could be easily quantified. These were swim speed (extrapolated from GPS position), synchronicity and directionality of the animals in the group during the surfacing, and the presence of aerial and percussive behaviours such as breaching (leaping clear or partially out of the water), spyhopping (surfacing vertically and lifting the head out of the water), as well as slapping the surface with the tail flukes or flippers. The following behaviour categories were used in this study (modified from Ford 1989; Barrett-Lennard *et al.* 1996):

- *Surface-active*: This behaviour category was characterised by frequent physical contact between members of the group, as well as occasional aerial and percussive behaviours including breaches, tail-slaps, pectoral slaps and spyhops. Surface-active whales typically moved at speeds of less than 6 km/h, did not surface in synchrony and frequently changed their direction.
- *Milling*: Milling whales moved at speeds of less than 3 km/h and lacked a clear direction. The dive sequences of individuals in the group were irregular and not synchronised and there were no aerial or percussive behaviours. Milling

behaviour observed after a confirmed or possible kill was not included in this category.

- *Milling after Kill*: This category described behaviours typically observed during and after a kill of a marine mammal. The dive pattern, directionality, and swim speed were similar to those during milling, but often included aerial and percussive behaviours. This behaviour ended when the whales increased their swim speed and moved away from the site of the kill. Only milling after a confirmed kill was included in this category.
- *Slow Travel*: During slow travel, the dive sequences of the animals in a group were synchronised and the animals consistently moved in the same direction for several surfacings. Swim speeds during slow travel ranged from three to 6 km/h.
- *Travel*: During travel, all members of a group surfaced in synchrony, and consistently moved in the same direction, usually within a few body lengths of each other. Swim speeds during travel exceeded 6 km/h.

I found that it was impossible to consistently identify when the whales were actively searching for prey. Therefore some behaviours classified as foraging by Barrett-Lennard *et al.* (1996) fall into the category Slow Travel in the present study.

2.2 Acoustic and Statistical Analysis

The recordings were visually and acoustically inspected for pulsed calls using the CoolEdit 2000 sound analysis package (Syntrillium Software). Pulsed calls were classified into discrete and variable calls (Ford 1989) and discrete calls were assigned to call types using the method described in Chapter V. While the underwater calls of resident killer whales can be heard over distances of many kilometres (Miller 2000a), the calls of transient killer whales are often faint. In order to minimise the number of missed calls, only the sections of an encounter when the whales were within 500 m of the hydrophone (*i.e.* between consecutive surfacings within 500 m of the boat) were included in the analysis. To quantify the level of vocal activity I calculated the rate of vocal behaviour (*r*) using the formula:

$$r = \frac{c}{t * i}$$

where *c* is the number of pulsed calls recorded while the animals were within 500 m of the boat, *t* is the time in minutes that the animals spent within 500 m of the boat and *i* is the number of individuals in the group. The unit for the rate of vocal behaviour therefore reflects calls per individual per minute.

To compare the level of vocal activity across the different behaviour categories, I calculated the rate of vocal behaviour for each behaviour category observed in a given encounter. This means that all data points within a behavioural category are independent, but some data points in different behaviour categories come from the same encounter. Since vocal rates from the same encounter are more likely to be similar and since I tested for difference between behaviour categories, this is a conservative approach. Transient killer whales were silent for most of the time (*i.e.* modal rate of vocal behaviour was zero) and all statistical tests were therefore non-parametric. To test for effects of the behavioural context on the level of vocal activity I used a Kruskal-Wallis test to test for differences across behaviour categories and used Dunn's multiple comparison with tied ranks and unequal sample size (Zar 1996) to identify homogeneous subsets.

To test whether vocal activity was significantly elevated after a kill, I compared levels of vocal activity while the animals were milling after the kill in the encounters where confirmed kills were observed with level of vocal activity for the other behaviour categories during the same encounters using a Wilcoxon signed ranks test. Except for Dunn's multiple comparison, which was calculated using the method outlined in Zar (1996), all statistical tests were done using the SPSS statistics package (SPSS Inc.).

2.3 Comparison with Resident Killer Whales

I determined levels of vocal activity during six encounters with groups of resident killer whales using the methodology described above to see whether transient killer whales vocalise less frequently than residents. Since resident groups tend to be more spread out than groups of transients, it was often unlikely that all members in a group would be within 500 m of the boat. Rates of vocal behaviour for resident killer whales were therefore calculated using the time and the number of calls recorded while at least one member of the group was within 500 m of the boat. Since the calls of resident killer whales can be heard over several kilometres (Miller 2000a) it is unlikely that a significant number of calls were missed; however, if calls were missed due to animals being outside of the range of acoustic detection, this would bias the rate of vocal behaviour downward, since the total number of animals in the group (and not animals within 500 m) were used to calculate this parameter. An overall rate of vocal activity across all behaviour categories was calculated for each encounter with transient killer whales and compared to the rates for residents using a Mann-Whitney U test (Zar 1996).

3 RESULTS

3.1 The Behavioural Context of Vocal Behaviour in Transient Killer Whales

A total of 23 groups of transients were encountered in the course of the study. Group size ranged from one to 18 animals (mean: 5.6, standard deviation: 4.6) and encounters lasted between 30 min and 483 min (mean: 191 min, standard deviation: 116 min). During an encounter, the animals spent between 2 min and 58 min (mean: 20 min, standard deviation: 14 min) within 500 m of the vessel. The number of acoustic samples and time spent within 500 m of the animals varied between behaviour categories: travel was observed in 15 encounters (total time of recording within 500 m:140 min), slow travel in 10 encounters (154 min), milling after a kill in six encounters (79 min), surface-active in four encounters (50 min), and milling in four encounters (12 min). The vocal rate was highest when the animals were surface-active (median call rate: 0.63 calls per individual per minute, interquartile range: 0.12-1.43) followed by milling after a kill (median: 0.27, interquartile range: 0.23-0.59). During all other behaviours, the animals were usually silent (median call rate: 0.00 calls per individual per minute, interquartile range: 0.00-0.00). The vocal rate differed between behaviour categories (Kruskal-Wallis test: $X^2_{4,34} = 18.50$, $p = 0.001$) and vocal behaviour while milling after a kill was significantly higher than during slow travel (Dunn's test: $Q = 2.94$, $p < 0.05$), travel ($Q = 3.25$, $p < 0.02$), and milling ($Q = 2.95$, $p < 0.05$). All other comparisons were not significant. These results are illustrated in Figure 5.

The results of the acoustic analysis are given in Figure 6. With the exception of one encounter, the animals produced three discrete calls (WCT01, WCT02, and WCT11) in addition to variable calls during the two behavioural states when significant amounts of vocal behaviour were recorded. During a single bout of surface-active behaviour (encounter 02-08-22) the animals frequently produced three additional call types (WCT03, WCT07 and WCT08) in addition to the more common WCT01, WCT02, and WCT11. Aside from this single encounter, visual inspection of the vocal repertoires shows no pronounced differences in the call types produced while the animals were surface-active compared to when they were milling after a kill.

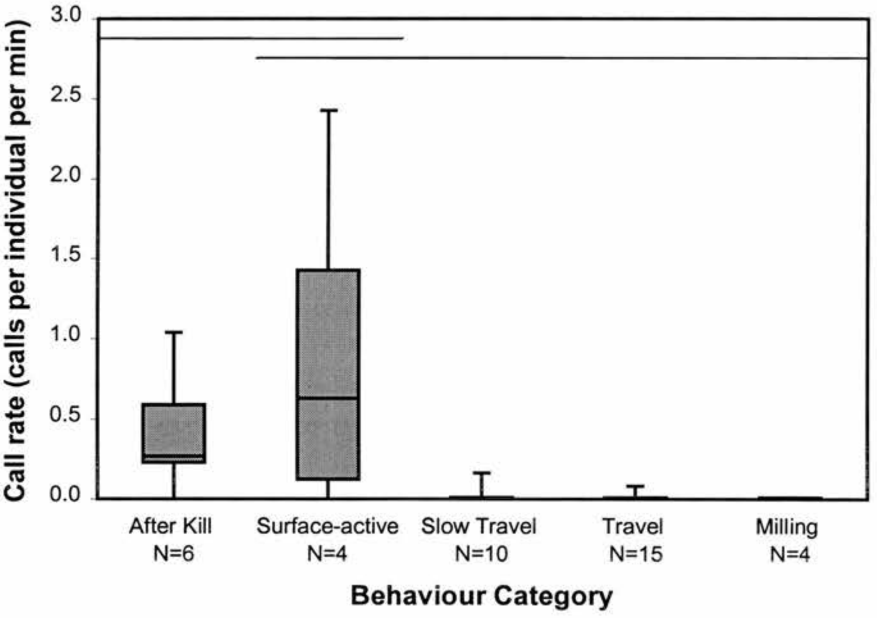
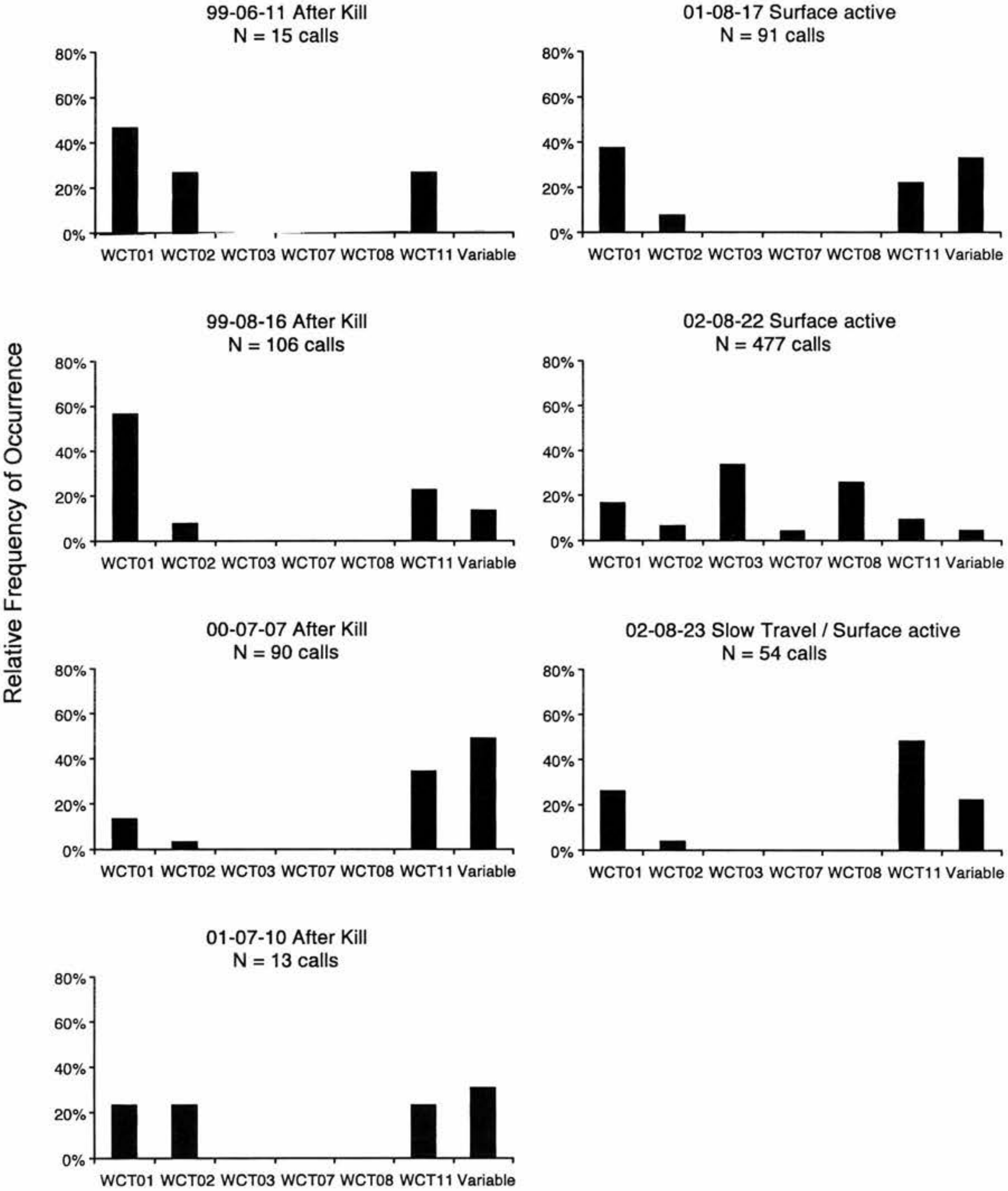


Figure 5: Differences in the rate of pulsed calls across behaviour categories in transient killer whales. Horizontal bars give median call rate, boxes show the interquartile range and whiskers give the full range of call rates. The level of vocal activity differs across behaviour categories (Kruskal-Wallis test: $X^2_{4,34} = 18.50$, $p = 0.001$). Horizontal lines delineate homogeneous subsets: all bars under the same line could not be distinguished statistically ($p > 0.05$).



99-06-11 After Kill
N = 15 calls

01-08-17 Surface active
N = 91 calls

99-08-16 After Kill
N = 106 calls

02-08-22 Surface active
N = 477 calls

00-07-07 After Kill
N = 90 calls

02-08-23 Slow Travel / Surface active
N = 54 calls

01-07-10 After Kill
N = 13 calls

Figure 6: Call repertoires of transient killer whales while milling after a marine mammal kill (left column) compared to other behavioural states. Alphanumeric designations starting with WCT (for West Coast transient) refer to call types (see Appendix III for sample spectrograms). Recording sessions are labelled in the format yy-mm-dd. Note the additional call types produced in encounter 02-08-22. Only sessions during which 10 or more pulsed calls were recorded are shown.

Table I: Group size and composition, prey species and vocal rate for the six confirmed attacks on marine mammals.

Date (yy-mm-dd)	**Individuals present**[1]	**Prey species**	**Vocal rate after kill** (calls per individual per minute)
99-06-11	T101, T101A, T101B, T102	not determined	1.04
99-06-15	T086, T086A, T103, T104	Dall's porpoise	0.27
99-08-16	T018, T019, T019B, T020, T021, T022	Dall's porpoise	0.69
99-09-16	T059, T059A, T060	not determined	0.00
00-07-07	T036, T036A, T036B, T063, T065, T065A, T065A1, T065B, T100, T100B, T101, T101A, T101B, T102	harbour seal	0.26
01-07-10	T090, T090A, T124A, T124A1, T124A2	harbour seal	0.12

[1] See Ford & Ellis (1999) for information on individuals.

3.2 Test for Food-Associated Calling

Successful attacks by transient killer whales on marine mammals could be confirmed during six of the 21 encounters. Details on these attacks are given in Table I. In an additional two encounters, indirect evidence (seagulls hovering above the whales, crunching noises on the hydrophone) indicated a possible marine mammal kill. The prey species could be identified for four of the six confirmed kills. With the exception of one kill of an unidentified marine mammal, the animals emitted pulsed calls while milling after the kill (median vocal rate: 0.27 calls per individual per minute, interquartile range: 0.23-0.59). No calls were recorded during any other behaviour categories in the same encounters (see Figure

7) and the difference in vocal rate while milling after a kill compared to the other behaviour categories is significant (Wilcoxon Test: $Z_5 = -2.02$, $p = 0.04$). This suggests that vocal activity is often associated with feeding in transient killer whales.

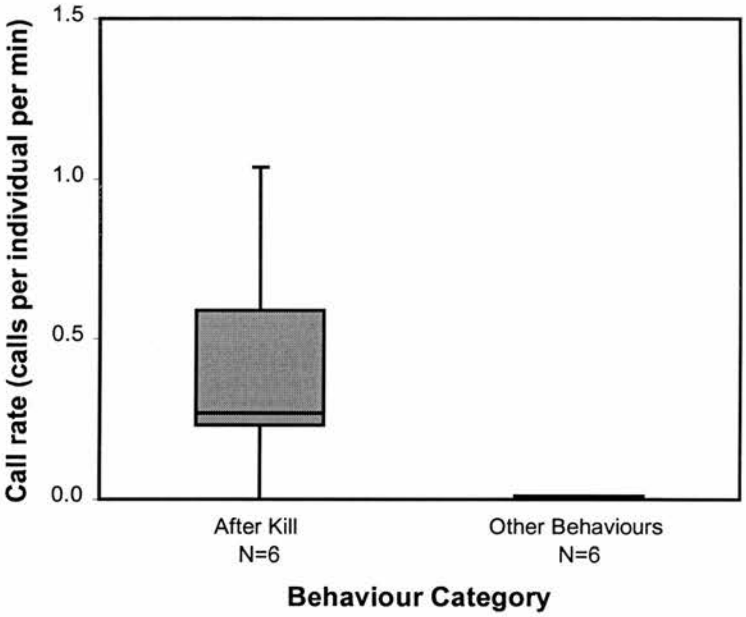


Figure 7: Differences in the number of pulsed calls recorded from transient killer whales when milling after a kill compared to all other behaviour categories from the six encounters during which confirmed kills of marine mammals were observed. Horizontal bars give median call rate, boxes show the interquartile range and whiskers give the full range of call rates. Levels of vocal behaviour are significantly higher after a successful attack (Wilcoxon Test: $Z_5 = -2.022$, $p = 0.043$).

3.3 Comparison with Resident Killer Whales

Data on the rate of pulsed calls emitted by resident killer whales were obtained during eight encounters with groups of residents. Group sizes for these encounters ranged from three to 22 animals (mean: 9.8, standard deviation: 6.6) and encounters lasted between 28 min and 403 min (mean: 108 min, standard deviation: 124 min). During encounters with resident killer whales, at least one animal was within 500 m of the hydrophone for between 4 min and 127 min (mean: 28 min, standard deviation: 40 min). Residents emitted pulsed calls more frequently than transient killer whales: median call rate across all behaviour categories for residents was 0.70 calls per individual per minute (interquartile range: 0.06 - 1.33) compared to 0.05 calls per individual per minute (interquartile range: 0.00 - 0.19) for transients (see Figure 8). In spite of the small sample size for resident killer whales, the difference in the call rate between the two ecotypes of killer whales is significant (Mann-Whitney test: $U_{30} = 46$, $p = 0.038$).

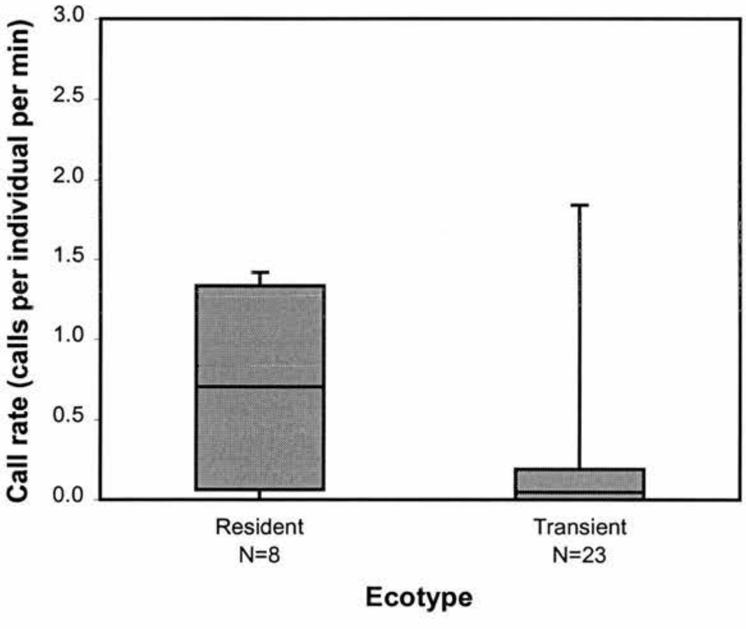


Figure 8: Differences in the rate of pulsed calls by fish-eating (resident) and mammal-eating (transient) killer whales across all behaviour categories. Horizontal bars give median call rate, boxes show the interquartile range and whiskers give the full range of call rates. Call rate differs significantly between resident and transient killer whales (Mann-Whitney test: $U_{30} = 46$, $p = 0.038$).

4 DISCUSSION

4.1 Food Calling or Food-associated Calling?

The results of this study show that vocal behaviour in transient killer whales occurs infrequently. With the exception of milling after a kill, the median call rate for all behaviour categories is zero, and even while surface-active the whales were completely silent in one out of four encounters. In resident killer whales, surface-active is the behavioural state characterised by the highest levels of vocal activity (Ford 1989). The comparison between the level of vocal activity of residents and transients shows that transient killer whales not only use echolocation less frequently than residents (Barrett-Lennard *et al.* 1996), but also emit significantly fewer pulsed calls.

Transients vocalised most frequently while milling after a marine mammal kill, and in the six encounters where kills could be confirmed, the levels of vocal activity were significantly elevated in this behavioural context. This shows a strong link between vocal activity and the presence of food in transient killer whales indicating that vocal behaviour in transient killer whales is to a high degree food-associated (in the sense of Janik 2000). However, the question remains whether this association indicates food-related signalling (informing conspecifics about the presence of food). Alternatively, vocal behaviour may be food-associated because it is part of the foraging process, because vocal communication is associated with increased levels of excitement after a kill (see Marler & Evans 1996) or is part of the social interactions during food-sharing, or because vocal behaviour carries a comparatively small cost in this behavioural context.

In contrast to the findings of Guinet (1992), there is no evidence that the vocal behaviour recorded in this study served to attract other killer whales. In no instance were other whales observed to join the focal group when it was vocal. Although measurements of the loudness of calls are needed to confirm this, most calls recorded in this study appeared rather faint compared to those of resident killer whales and may not be detectable by other killer whales over the large distances reported by Miller (2000a). In one encounter (00-07-07), 14 transients were travelling in two subgroups separated by approximately 500 m. The trailing group caught a harbour seal and produced many pulsed calls (call types WCT01, WCT02, and WCT11, see Figure 6) during and after the kill. The leading group, however, did not rejoin them even though they were probably within acoustic range of the vocalising animals. It therefore seems unlikely that this type of vocal behaviour functions to attract other individuals to the site of a kill. It cannot be ruled out, however, that other, louder call types may function as contact calls.

In another encounter (02-08-22) a second group, that was 30 km distant from the focal group, killed a Dall's porpoise and started vocalising after the kill (Graeme M. Ellis, pers. comm). The focal group became vocal at the same time, producing call types WCT03, WCT07, and WCT08, as well as the common call types WCT01, WCT02, and WCT011 (see Figure 6). Both groups eventually joined up two hours later 19 km from the site of the kill, with the group involved in the kill having covered the majority of the distance. It is unclear whether the two groups were in acoustic contact at the time of the kill although, given the rarity of vocal behaviour in transient killer whales, the coincidence of vocal activity in two groups is remarkable. Using measured source levels and data on hearing acuity from captive animals, Miller (2000a) estimated that resident killer whales can detect each others calls over a maximum distance of 25 km. If the two groups were in acoustic contact, it was the group that had killed the porpoise that left the site of the kill to join the other group, which makes a case against food calling in this encounter.

Several functions have been proposed for food-related signalling in birds and mammals, but many of these are of limited applicability to the situation in transient killer whales. Hauser & Marler (1993) argued that food calling could serve to alert related animals to the presence of food and thus increase an individual's inclusive fitness. Social groups of transient killer whales consist of individuals that are maternally related (Ford & Ellis 1999). Attacks by transients are coordinated and all members of a social group are usually present during an attack, either participating actively or as bystanders (Jefferson *et al.* 1991; Ford *et al.* 1998). Vocalising if the attack is successful therefore is more likely to attract unrelated individuals rather than additional relatives. On the other hand, attraction of potential mates to the site of a food source (*e.g.*, Stokes & Williams 1972; Van Krunkelsven *et al.* 1996) may be a possible function of vocal behaviour in transient killer whales, although, as explained above, most of the recorded calls were probably too faint to cover any large distance. It cannot be ruled out, however, that other, louder call types may serve this function.

In many birds and primates, attracting other individuals to a food source is thought to decrease the risk of predation, and to allow the signaller to spend more time foraging and less time on vigilance (*e.g.*, Elgar 1986; Chapman & Lefebvre 1990). Killer whales have no natural predators, and decreased risk of predation is therefore is not applicable as an explanation for food-associated calling. There is evidence for aggression between the resident and transient ecotypes (Ford & Ellis 1999) and possibly evidence for cannibalism among killer whales (Rice 1968), but vocal behaviour is as likely to attract aggressors as affiliative individuals. Marzluff & Heinrich (1991) argued that food calling in ravens may function to attract social companions to a carcass and thus to increase the chance of overcoming the defence of dominant individuals. In the Southern Ocean, C. Guinet (*pers. comm.*) has witnessed social groups of killer whales displacing others from a kill, but such antagonistic behaviours are not known from the North Pacific. Again, vocal behaviour after a kill would be equally likely to attract aggressive rather than affiliative individuals, and the best strategy to prevent scavenging would be to avoid detection altogether by remaining silent.

Since the calls were usually rather faint, did not appear to attract other killer whales to the site of a kill, and since there is no obvious benefit for food calling in transient killer whales, it is unlikely that the animals recorded in this study called to signal of the presence of food. The fact that the vocal behaviour always continued after the prey was dead, and that often no calls were recorded before the prey was killed, furthermore provides support that the vocal behaviour did not serve to manipulate the behaviour of the prey. The most parsimonious explanations for why transients vocalise after a kill are therefore increased excitement levels after a kill, within-group communication as part of social interactions during food-sharing, or a relatively low cost for vocal behaviour after a successful attack. After a kill the animals are satiated, and may not need to hunt again for some time, so that alerting potential prey animals in the immediate area does not carry a high cost. In addition, since attacks on marine mammals are usually accompanied with fast swimming, aerial behaviours and hitting or ramming the prey, the attacks themselves are noisy. Other potential prey animals in the area may therefore already be aware that killer whales are nearby, so that there is no additional cost for vocalising.

4.2 Strategies to Avoid Detection by the Prey: Reduction of Communication or Frequency Shift?

In predator-prey systems where the ecological cost of vocal behaviour is high, selection may favour vocalisations at frequencies in one party that are not detectable by the other. For example, some bats that feed on insects, which they locate by echolocation appear to avoid detection through the use of echolocation signals with frequencies outside of the range of best hearing of their prey (Rydell & Arlettaz 1994; Fullard & Dawson 1997; Pavey & Burwell 1998). Evolving echolocation signals of relatively low frequencies carries an associated cost: in order to be detectable by echolocation, an object must be at least as large as the wavelength of the echolocation signal. For low-frequency bats, the benefit of being relatively undetectable by tympanate insects therefore comes at the cost of only being able to detect relatively large prey (Rydell & Arlettaz 1994; Fullard & Dawson 1997). Other bats appear to be able to prey on tympanate insects by using echolocation signals above the insects' range of best hearing (Pavey & Burwell 1998). Since, compared to a low-frequency sound, a high-frequency sound of the same amplitude experiences a greater degree of attenuation, the cost in this situation lies in a decreased detection range or greater energetic cost of vocalising.

In theory, transient killer whales may be able to avoid detection by their prey by vocalising at frequencies that are inaudible to other cetaceans or to pinnipeds. The area of best hearing of killer whales lies between 18 and 42 kHz (Szymanski *et al.* 1999), and much of the energy of killer whale vocal communication is concentrated in this frequency band (Miller 2000a). Shifting the frequency band used by killer whales for communication to higher frequencies would decrease the distance over which calls could be heard and increase the energetic costs for vocalising due to increased attenuation and the higher cost of generating high-frequency sounds. In addition, two common prey species, the Pacific white-sided dolphins and the harbour porpoise and have excellent high-frequency hearing (up to 128and 140 kHz respectively; Tremel *et al.* 1998; Kastelein *et al.* 2002), so that any upward shift in the frequency of communication would have to be substantial in order to avoid detection. Restricting communication to low frequencies would eliminate directional cues, since the long wavelengths of such sounds could not be focussed by the melon (fatty tissue on the rostrum of cetaceans thought to act as an acoustic lens). Directional cues are potentially an important aspect of killer whale vocal communication (Miller 2000a). Harbour seals, California sea lions, and presumably Steller sea lions, all have good underwater hearing as low as 1 kHz (Schusterman *et al.* 1972; Wolski *et al.* 2003), so that again, any downward shift in frequency would have to be substantial. It therefore appears that limiting vocal communication is the only strategy to minimise detection by all potential prey.

CHAPTER IV - Learning What Not to Fear: Selective Habituation Shapes Acoustic Predator Recognition in Harbour Seals

1 INTRODUCTION

1.1 The Cost of Vocal Behaviour in Predator-Prey Interactions

The cost of vocal communication is usually expressed in energetic terms alone. However, animals often pay additional ecological costs for vocalising. For predatory animals, such costs include warning potential prey of their presence, and thus decreasing their chance of a successful attack. For prey animals, a major cost of vocal behaviour consists of alerting predators to their presence and hence increasing the probability of detection and attack (see Lima & Dill 1990).

Ecological costs for vocal behaviour are only incurred by predators if the prey is physiologically able to hear the vocalisations of the predator and responds to the vocalisations in a way that reduces the chance of its detection and capture (e.g., increased vigilance, movement to a safe refuge, *etc.*, see Lima & Dill 1990). In a situation where different populations of the same predatory species specialise on prey animals with differential hearing capabilities, predators focussing on prey with acute hearing in the frequency range of the predator's vocal communication will pay a higher price for vocal behaviour than predators specialising on prey with poor hearing capabilities. Assuming the benefits of vocal communication are equal in both populations, the difference in cost should lead to lower levels of vocal activity in the predator population hunting acoustically sensitive prey.

1.2 The Benefits of Precise Predator Identification

Predation is a major selective force on the behaviour of prey animals (Ydenberg & Dill 1986; Lima & Dill 1990). Correct identification of predators combined with appropriate anti-predator behaviour can confer substantial selective advantages on animals which serve as food for others (Curio 1993). While the costs of having a predator image that is too specific, thus causing the animals to fail to recognise a predator, are obvious, having a predator image that is too general is also costly as it would cause an animal to respond to nonexistent predatory threats. This is because anti-predator behaviour has associated fitness costs, either in the form of direct energy expenditure for locomotion (Ydenberg & Dill 1986) or by taking up time that could otherwise be used for reproduction or to find food (Curio 1993). Ideally, therefore, animals should develop a predator image that is general enough to cause them to respond to any real predatory threat and specific enough to exclude all harmless stimuli.

Having a learned component to predator recognition allows prey animals to respond faster to changes in the predatory threat (Curio 1993). Learning may shape an individual's predator image in several ways. First, it is possible that animals start with rather specific predator images to which they add new predator types through associative learning. Such refinement of predator images through learning has been demonstrated experimentally in several species of birds and mammals (*e.g.*, Kramer & von St. Paul 1951; Curio *et al.* 1978a; Curio *et al.* 1978b;

Shriner 1999; Griffin *et al.* 2001). Secondly, animals could begin with rather general predator images, which are rendered more precise by selective habituation to stimuli which are never paired with any predatory threat. That is, animals learn which stimuli not to fear. Schleidt (1961) postulated a related mechanism, the rarity principle, which suggests that animals begin with a general predator image that includes all potentially dangerous objects, but selectively habituate to stimuli that they experience frequently. Since predators are by necessity rare in the environment, true predatory threats are thereby excluded from habituation.

1.3 Killer Whale Ecotypes in the Northeastern Pacific

The Northeastern Pacific is home to two distinct ecotypes of killer whales, which differ in a variety of aspects of their ecology, social structure and behaviour. Resident killer whales live in large stable groups and feed exclusively on fish, preferentially on chinook salmon *(Oncorhynchus tshawytscha*). Transients, on the other hand, live in smaller social groups and feed on marine mammals and sometimes seabirds (Ford *et al.* 1998; Saulitis *et al.* 2000). Killer whales from different ecotypes do not interbreed in the wild and rarely interact. Resident killer whales along the west coast of North America fall into three distinct populations: Alaskan residents inhabit the waters of Prince William Sound and Southeast Alaska. Northern residents range from central Vancouver Island into Southeast Alaska, and Southern residents inhabit the waters from Washington State to central Vancouver Island. West Coast transients are sympatric with residents and form a continuous population from northern California to Southeast Alaska (Ford & Ellis 1999; Matkin *et al.* 1999; Ford *et al.* 2000).

The two ecotypes of killer whale show striking differences in their vocal behaviour. Residents specialise on salmon, a prey with poor underwater hearing (Hawkins & Johnstone 1978), and frequently emit echolocation clicks and communicative calls. Transients, on the other hand, specialise on marine mammals, a prey with excellent underwater hearing, and are usually silent (Felleman *et al.* 1988; Ford 1989; Barrett-Lennard *et al.* 1996). Resident killer whales have a complex system of vocal dialects in which different matrilineal social groups have different repertoires of highly stereotyped discrete call types. Ford (1991) placed all social groups that share at least one such call type into a common acoustic clan. By this definition, the Alaskan resident population contains two clans, the Northern resident population contains three clans, and the Southern resident population is comprised of a single acoustic clan (Ford 1991; Yurk *et al.* 2002). By contrast, repertoire variation among West Coast transients is much smaller and all members of this population share several call types (Ford 1984; see Chapter V).

1.4 Objectives

Harbour seals are a preferred prey of transient killer whales in the coastal waters of southern British Columbia, Canada (Ford *et al.* 1998), and have good underwater hearing at the frequencies of killer whale vocal communication (Wolski *et al.* 2003). Harbours seals have been shown to respond to visual cues associated with terrestrial predators (Nordstrom 2002). Since killer whale calls can be heard over long distances, it would be beneficial for harbour seals to recognise the calls of transients and to respond with anti-predator behaviour. When salmon migrate through these waters, individual groups of resident killer whales, that pose no predatory threat to seals, will often spend several weeks in a relatively small geographic area (Nichol & Shackleton 1996). Seals living in these areas would be paying a high cost in terms of increased energy expenditure, decreased energy intake or missed chances for reproduction if they responded to all killer whale calls indiscriminately. For this reason, it would benefit harbour seals to have rather precise recognition of killer whale calls. However, given the complexity of killer whale vocal communication, especially of the resident dialect system, consistent discrimination between calls of residents and those of transients represents a formidable learning task.

The first objective of this study was to test whether harbour seals respond to calls of transient killer whales using a paired playback design. If calls elicit anti-predator behaviour in a preferred prey species, this would demonstrate an ecological cost for vocal behaviour in transient killer whales, and would in turn make a case for this cost being the reason for the difference in vocal activity between residents and transients. Secondly, I wanted to find out whether seals are able to distinguish between harmless and dangerous killer whales by their calls and whether they response to the calls of residents and transients differs. Finally, if seals responded differently, I wanted to know if this difference is caused by associative learning - learning to associate the calls of transients with danger - or by selective habituation to the frequently heard calls of the harmless residents. These two mechanisms of fine-tuning responses to predator-associated cues can be separated by assessing the response of harbour seals to the calls of unfamiliar killer whales. If seals generally do not respond to the calls of killer whales, but have learned to associate the calls of transients with a predatory threat, seals should only show a weak response to the calls of unfamiliar killer whales. If, on the other hand, seals generally respond to killer whale calls but have selectively habituated to the calls of residents, I predict a strong anti-predator response to unfamiliar killer whale calls.

2 METHODS

2.1 General Playback Procedure

I addressed these questions in two playback experiments conducted in the summers (June to September) of 2000 and 2001. Playbacks were performed to harbour seals in the water near reefs where seals haul out onto land using a TCD-D8 DAT-recorder (Sony) and an LL916 underwater speaker (Lubell Labs) deployed at a depth of approximately 5 m from a small boat (6 m aluminium vessel or 4 m inflatable). Maximum source level of the loudest call in each sequence was 147.5 dB re 1 μPa @ 1 m. This is 5.1 dB lower than the average loudness of discrete calls of resident killer whales (Miller 2000a) and corresponds to a whale calling several kilometres away.

On arrival at the study sites, the boat was anchored about 100 m from the haulout, at which time many seals entered the water, but remained close to the haulout, often inspecting the boat at close range. I counted the number of seals in the water within our visual field and measured the distance to the nearest animal at 20 s intervals for at least two minutes preceding the playback of the calls. I played the 1 min playback sequence a single time and continued to note the number of animals and distance to the nearest animal for an additional two minutes or more. The average number of seals at the surface before playbacks was 12.73 (standard deviation: 6.94). Trials where less than five seals were present before the playback were excluded from the analysis. The strength of the response was expressed as the effect size, that is the percent change in the average number of seals and the average distance to the nearest seal from the two minutes before to the two minutes after the calls played. Playback experiments were conducted off northern Vancouver Island in Johnstone and Queen Charlotte Strait and off southern Vancouver Island in Haro and Georgia Strait.

2.2 Experiment 1: Do Harbour Seals Respond to Calls of Transients?

In this experiment I used a paired playback design playing both treatment and control sequences at eight different seal haulouts. Treatment and control playbacks were conducted once each at the same haulout in random order with a roughly 25 hr time interval between them (*i.e.* at the same tidal height on consecutive days). Both kinds of playback sequences included sections of background noise (*i.e.* sections between the calls) from a recording of West Coast transient killer whales that were digitally spliced into a 1 min sequence (a 1 s cross-fade between sections prevented high-frequency artefacts). Sections containing whistles, echolocation clicks or pulsed calls were not used for this purpose. For treatment sequences, five discrete killer whale calls from the same recording belonging to at least three different call types were spliced into the sequence, for control sequences an additional five sections of background noise were spliced in instead of the calls.

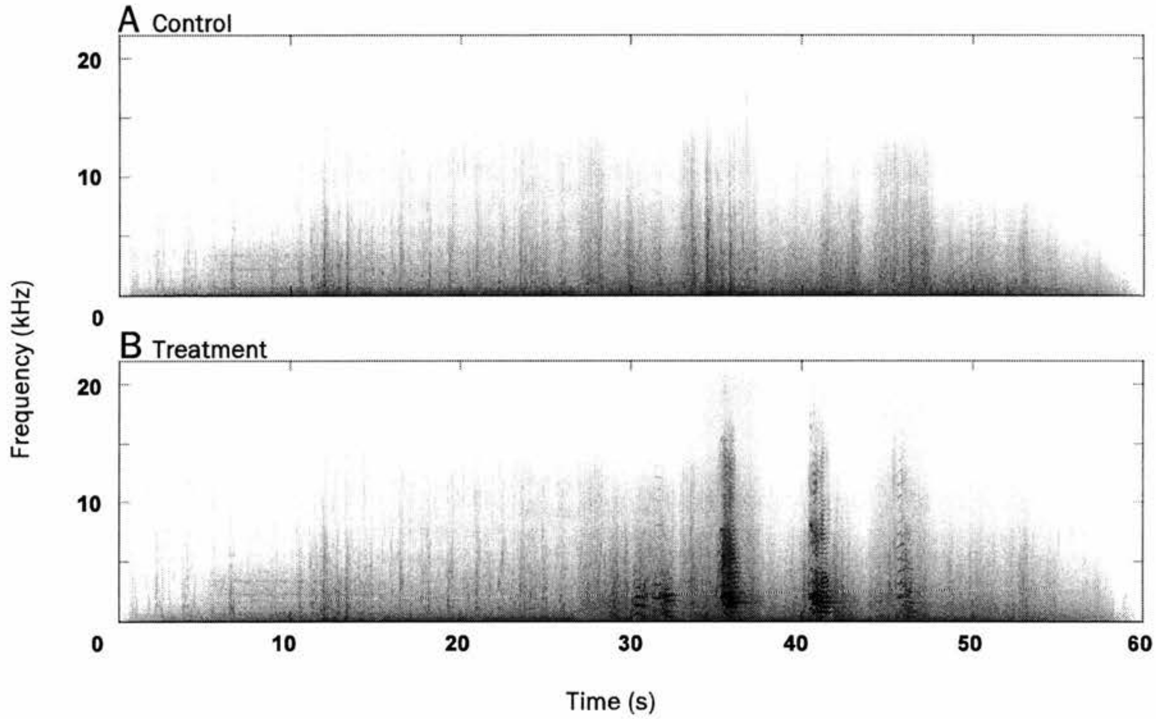


Figure 9: Spectrograms of a pair of playback sequences used to determine if harbour seals respond to the calls of transient killer whales. Panel A: Control sequence. Panel B: treatment sequence. Note that the two sequences are identical except for the five killer whale calls in the treatment sequence. Four such sequence pairs were used in the experiment. See Panel A of Figure 10 for a close-up of section of the treatment sequence containing the calls.

To avoid startle responses caused by the sudden onset of unfamiliar background noise, the sequences were slowly faded in over the first 30 s and faded out during the last 10 s. The 20 s section between the fades in the treatment sequence contained the killer whale calls. See Figure 9 for an example of a pair of playback sequences. The digital sound editing was done using the GoldWave 4.11 sound analysis software (GoldWave Inc.). I generated and used four such sequence pairs from recordings of different transient groups. In order to avoid pseudoreplication (Kroodsma 1989), I averaged responses obtained at the two haulouts where the same pair of playback sequences was played, so that statistical degrees of freedom are determined by the number of playback sequences and not by the total number of playbacks. I used one-sample T-tests to test whether responses were significant (*i.e.* effect sizes differed from zero) and a paired T-test to test for significant differences between responses to treatment and control.

2.3 Experiment 2: Do Harbour Seals Discriminate Between Calls of Different Killer Whales?

For this experiment, I generated three types of playback sequence using the methodology explained above. Sequences for playbacks of familiar fish-eating calls contained five calls from BC resident killer whales. For playbacks off northern Vancouver Island, recordings of members of A-clan from the Northern resident population were used. Members of this clan are most frequently encountered in the waters where the playbacks were conducted. For playbacks off southern Vancouver Island, recordings of members of J-Clan, the only acoustic clan in the Southern resident population were used instead. For playbacks of unfamiliar killer whale calls I generated sequences from recordings of Alaskan residents. These killer whales are ecologically and genetically very similar to the BC residents but are not known to venture south of the Alaskan border with British Columbia, some 600 km north of our study area, and are therefore unfamiliar to harbour seals in southern British Columbia. Sequences of transient calls were those used as treatment sequences in Experiment 1. See Figure 10 for examples of playback sequences used.

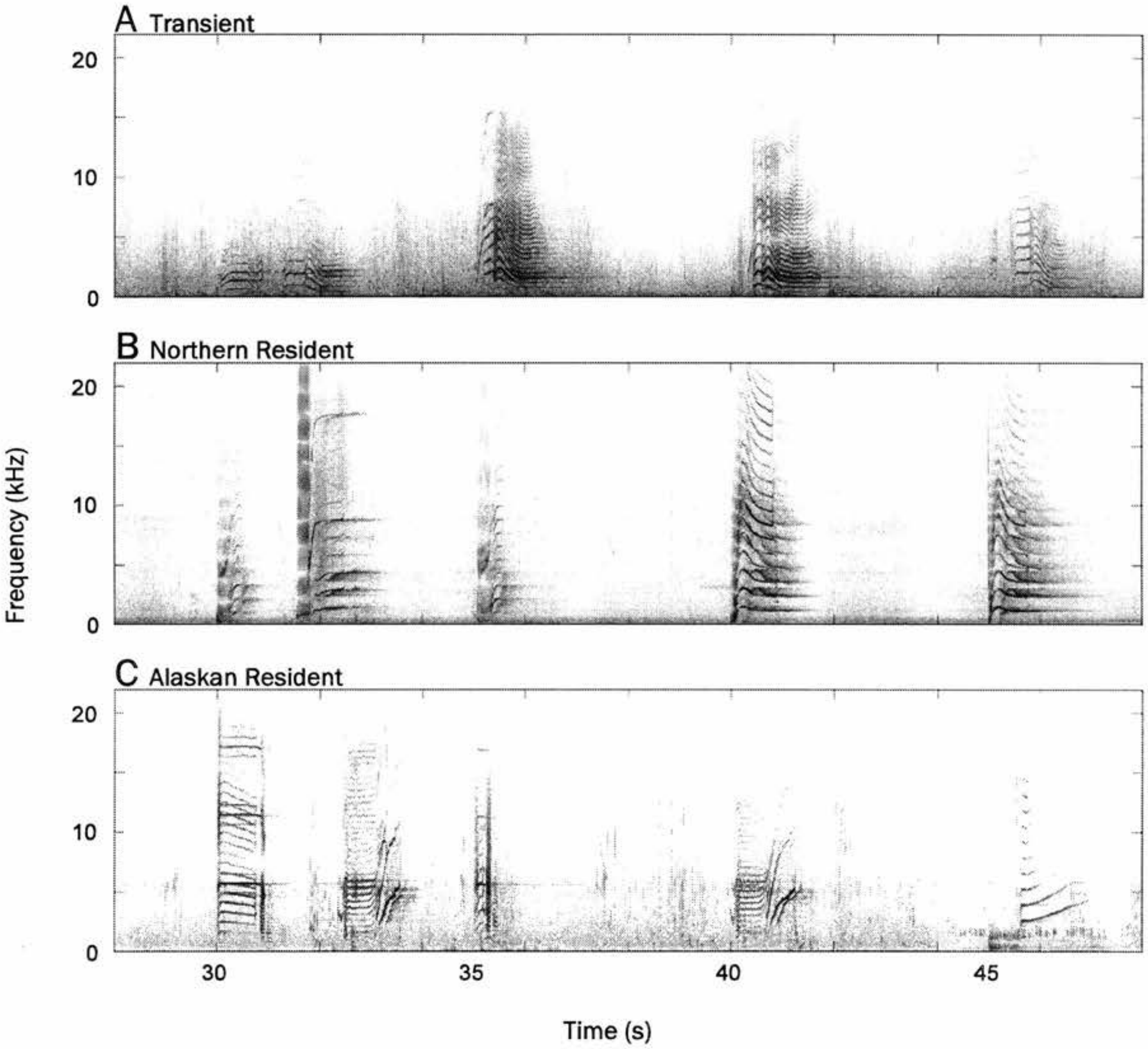


Figure 10: Spectrograms of sections (*t* = 28 s to *t* = 48 s) of playback sequences used to investigate the response of harbour seals to the calls of different killer whales. Panel A: mammal-eating killer whales (West Coast transients). Panel B: Familiar fish-eating killer whales (Northern residents). Panel C: Unfamiliar fish-eating killer whales (Alaskan residents). Four such playback sequences were used for each playback type.

Except for the familiar fish-eating killer whales I generated four sequences for each playback type from recordings of different social groups of killer whales. For familiar fish-eating killer whales, I generated a total of seven playback sequences, three of which were used off northern Vancouver Island and four in Haro Strait. Haulouts where playback had been conducted for Experiment 1 were not used again. As before, to avoid pseudoreplication, all responses obtained with the same playback sequence were averaged. I again used one-sample T-tests to test whether responses were significant. I used a one-way ANOVA to test for statistical differences between the playback types and used Tukey's honestly significant difference test (Zar 1996) to determine which playback types differed.

3 RESULTS

3.1 Experiment 1

Seals in the water responded to playbacks of killer whale calls primarily by diving. In no case did seals haul out on land in response to a playback. The reduction in the number of seals at the surface was generally short lived and seal numbers usually returned to pre-playback levels after 5-10 min. However, when seals returned to the surface, they were often in shallow water or in beds of bull kelp (*Nereocystis* sp.). In two cases, all seals resurfaced in a narrow surge channel near the haulout. The results are shown in Figure 11 and responses at individual haulouts are given in Appendix I (Table A-I). Counts of harbour seals changed on average by -49% (range: -73% to -24%) after playback of sequences containing calls of mammal-eating killer whales, a change which is significantly different from zero (one-sample t-test, $t_3 = -9.56$, $p < 0.01$). After control playbacks, seal numbers changed on average by -8% (range: -39% to 28%). This change is not significantly different from zero (one-sample t-test, $t_3 = -2.20$, $p = 0.11$). The difference in the numeric response between treatment and control is significant (paired samples t-test, $t_{1,3} = -6.77$, $p < 0.01$). The distance of the nearest seal to the playback source after treatment playbacks increased on average by 25% (range -17% to 115%) compared to 14% (range: -17% to 66%) after control playbacks. Both effect sizes do not differ significantly from zero (one-sample t-test, treatment: $t_3 = 2.14$, $p = 0.12$, control: $t_3 = 1.86$, $p = 0.16$), and the difference between treatment and control is not significant for this measure (paired samples t-test, $t_{1,3} = 0.83$, $p = 0.47$).

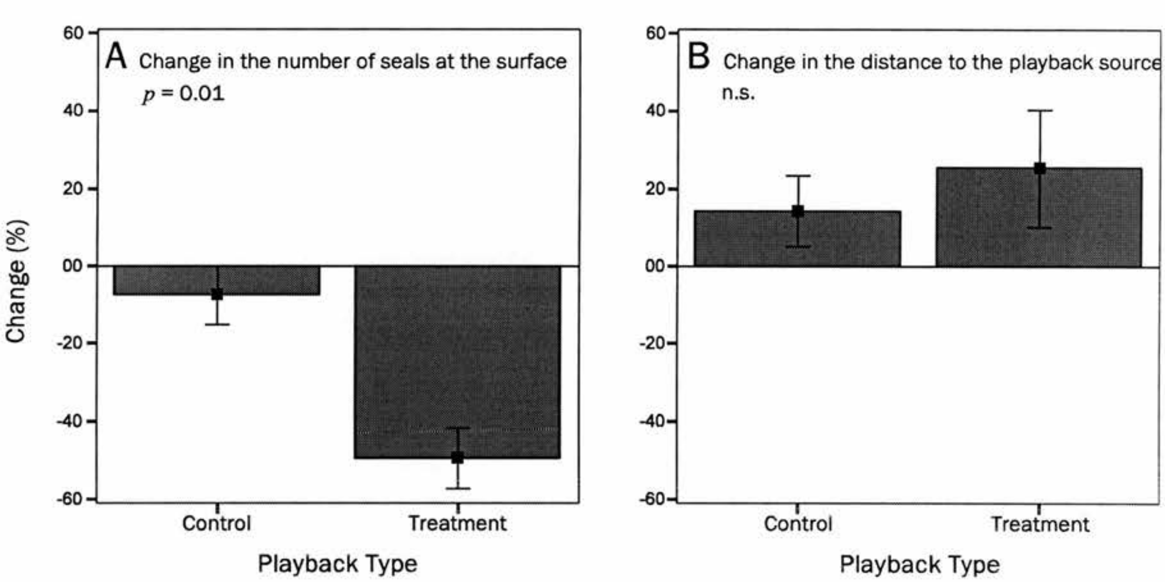


Figure 11: Results of the playback experiment to determine whether harbour seals respond to the calls of transient killer whales. Bar graphs give the change in the number of seals visible at the surface (panel A) and the distance of the nearest seal to the playback source (panel B) after treatment and control playbacks at eight different seal haulouts. Error bars give mean ± 1 *S.E.*

3.2 Experiment 2

The results of Experiment 2 are shown in Figure 12 and responses at individual haulouts are given in Appendix I (Table A-II). Seals again showed a strong tendency to dive after hearing calls of mammal-eating killer whales. Seal numbers at the surface changed on average by -44% (range: -71% to -10%) after playback of calls of transient killer whales. Seal numbers only changed slightly after playback of familiar fish-eating killer whales (average: -2%, range: -41 % to 37%). However, seal numbers at the surface exhibited a strong decline in response to the calls of unfamiliar fish-eating killer whales (-47%, range: -79% to -28%). The change in numbers after playbacks of calls of mammal-eating and unfamiliar fish-eating killer whales is significantly different from zero (one-sample t-test, mammal-eating killer whales: $t_3 = -5.74$, $p = 0.01$, unfamiliar fish-eating killer whales: $t_3 = -22.36$, $p < 0.01$),while the response to playbacks of calls of familiar fish-eating killer whales is not significantly different from zero (one-sample t-test, $t_6 = -0.75$, $p = 0.48$). The differences in the response to the three types of playback are statistically significant (ANOVA, $F_{2,12} = 12.11$, $p < 0.01$) with the response to the calls of familiar fish-eating killer whales being significantly smaller than the response to calls of mammal-eating killer whales (Tukey's test, $p < 0.01$) and to calls of unfamiliar fish-eating killer whales (Tukey's test, $p < 0.01$). The responses to calls of mammal-eating and unfamiliar fish-eating killer whales were statistically indistinguishable (Tukey's test, $p = 0.992$). The distance of the nearest seal to the playback source increased by 12% (range: -19% to 46%) after playbacks of calls of mammal-eating killer whales, changed by -2% (range: -32% to 26%) after playbacks of calls of familiar fish-eating killer whales and increased by 4% (range -58% to 27%) after playback of calls of unfamiliar fish-eating killer whales. However, none of these changes are significantly different from zero (one-sample t-test, mammal-eating killer whales: $t_3 = 1.522$, $p = 0.225$, familiar fish-eating killer whales: $t_6 = 0.016$, $p = 0.988$, unfamiliar fish-eating killer whales: $t_3 = 0.446$, $p = 0.666$) nor are the differences across the three types of playback significant for this measure (ANOVA, $F_{2,12} = 0.685, p = 0.523$).

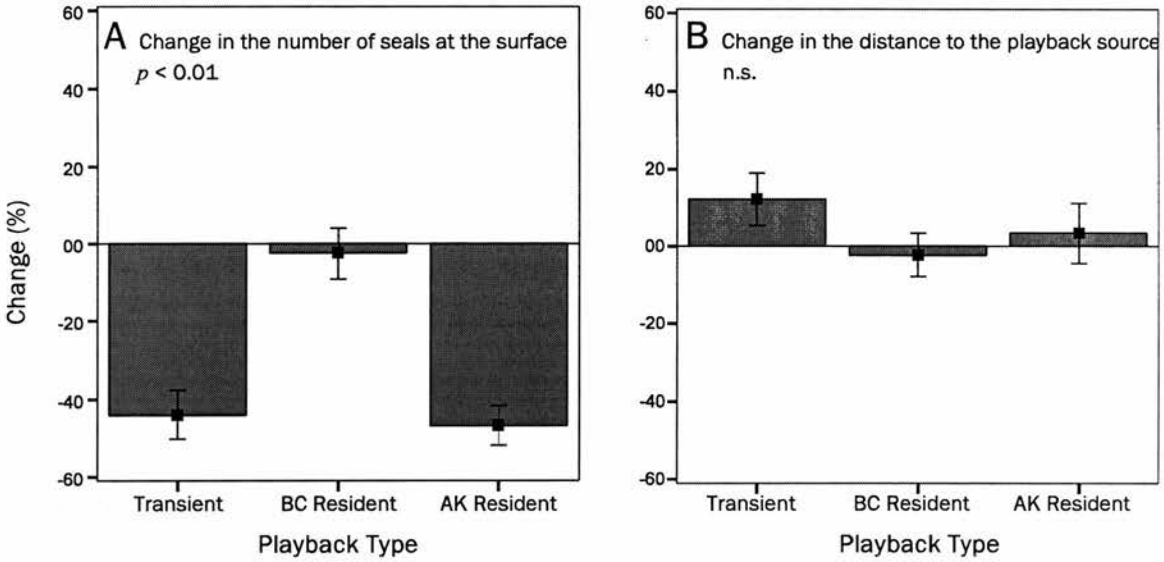


Figure 12: Results of the playback experiments to investigate the response of harbour seals to the calls of different killer whales. Bar graphs give the change in the number of seals visible at the surface (panel A) and the distance of the nearest seal to the playback source (panel B) after playbacks of calls of mammal-eating (Transient), familiar fish-eating (BC Resident) and unfamiliar fish-eating (AK Resident) killer whales. Sample size is 10 replicates for each playback type. Error bars give mean ± 1 *S.E.*

4 DISCUSSION

4.1 The Cost of Vocal Behaviour in Transient Killer Whales

The results of Experiment 1 show that harbour seals alter their behaviour after hearing the calls of transient killer whales. The paired treatment and control sequences used in this experiment were identical except for the killer whale calls (see Figure 9). The experimental design therefore controlled for extraneous stimuli such as cryptic echolocation clicks, background noise, or artefacts generated by the splicing procedure or the playback equipment. Seals responded primarily by diving and not by moving away from the playback source. The fact that I failed to find changes in the distance of the nearest seal from the playback source may be due to seal movements not being primarily directed away from the playback source, but toward locations that offered a refuge from predators (such as kelp beds, shallow areas, or surge channels). Diving may be an effective anti-predator behaviour for the following reasons: first, by submerging their heads, seals focus their vision and hearing to underwater stimuli and are therefore more likely to detect the approach of an aquatic predator. Secondly, seals at the water surface are highly visible to any predator coming from below and probably also provide a good echolocation target. By moving away from the water surface and possibly hiding on the bottom, seals can render themselves more cryptic to a predator hunting by vision or echolocation. Combined with the observation that seals often resurfaced in places inaccessible to killer whales, this suggests that transient killer whales pay a substantial price for vocal behaviour when hunting harbour seals. Harbour seals are a preferred prey of transients in many parts of their range. In addition to harbour seals, transients prey on a variety of cetaceans and pinnipeds (Ford *et al.* 1998; Saulitis *et al.* 2000). All of these species possess good underwater hearing at the frequencies of the pulsed calls of killer whales and are therefore likely to respond to the calls of transients, although this has yet to be demonstrated experimentally.

As with any behavioural trait, the frequency of occurrence of vocal behaviour should depend upon its fitness costs and benefits. While the benefits of vocal communication in killer whales remain poorly understood, possible functions include maintenance of group cohesion, as well as coordination of movements, activity levels, and behaviour in the group (Ford 1989; Miller 2000a). Arguably, these benefits are similar for resident and transient killer whales. The asymmetry in the cost of vocal behaviour between residents and transients, due to the difference in the hearing ability of their respective prey is therefore the most likely explanation for the difference in the frequency of occurrence of vocal behaviour between the two killer whale ecotypes.

4.2 Decoding the Vocal Variation of Killer Whales

The results of Experiment 2 show that harbour seals responded differently to the calls of mammal-eating killer whales and familiar fish-eating killer whales. The change of -43% in seal numbers after the playback of transient calls is comparable to that after treatment playbacks in Experiment 1 (-49%). The change of -2% after playback of calls of familiar fish-eating killer whales is somewhat less than the change after control playbacks in Experiment 1 (-8%). Given the large variance in the response, this is probably of no significance. Alternatively it could be caused by differences in the experimental design, or could indicate inspection behaviour by the seals (note that only playbacks of calls of familiar fish-eating killer whales caused a decrease, although not significant, in the distance of the nearest seal to the playback source).

The difference in the response of harbour seals to the calls of dangerous transients and harmless residents suggests that seals are able to use vocal differences between ecotypes of killer whales to assess the threat of predation. Due to the complexity of killer whale vocal communication, this is not a small feat: whereas the West Coast transient population is characterised by vocal conformity and most of the call types are shared among its members, resident killer whales have an intricate system of vocal dialects. Ford (1991) described 44 call types for the northern resident population and 26 call types for the southern resident population. Each matriline in these populations produces between seven and 17 call types (Ford 1989) with varying amounts of sharing between groups. Since some matrilines within the northern resident population have no call types in common, the amount of variation at the level of the repertoire within this population is as great as the difference between populations and ecotypes.

To ensure that the seals I studied had an opportunity for learning, I performed our experiments deliberately in areas where resident killer whales were frequent and, in the case of playbacks off northern Vancouver Island, used recordings of groups that were common in those areas. Extending the study to areas where resident killer whales are seen only occasionally or using recordings of groups that only enter the study area sporadically would be useful to delineate the extent to which harbour seals are familiar with the calls of resident killer whales.

4.3 Trade-offs in Predator Recognition - Risking a Life or Risking a Dinner

The results of Experiment 2 show that harbour seals respond equally to the calls of unfamiliar killer whales as they do to the calls of local mammal-eating killer whales. The unfamiliar killer whale calls used in this experiment were those of fish-eating killer whales from Alaska. These killer whales would have been harmless to the seals, although the seals had no opportunity to learn this, since Alaskan resident killer whales have never been observed in BC waters, and individual Pacific harbour seals are unlikely to travel over such distances (Lowry *et al.* 2001). The fact that I used calls from fish-eating killer whales that are genetically and ecologically very similar to BC residents rather than transients rules out the possibility that seals could have used shared features common to the calls of mammal-eating killer whale to classify these unknown killer whales as dangerous. The difference in the seals' familiarity with calls of the two resident groups is therefore is the only factor that can explain the observed patterns of response.

The strong response to the calls of unfamiliar killer whales implicates selective habituation rather than associative learning as the behavioural mechanism for fine-tuning the responses of harbour seals to different killer whale calls. This is in spite of the fact that learning to recognise the few call types of the transient population would be an easier task than becoming familiar with the multitude of call types of the resident dialect system. Selective habituation predicts that prey animals begin with a rather general predator image from which certain harmless stimuli are removed by habituation. In our case this hypothesis suggested that harbour seals generally do respond to all killer whale calls, but that they have become habituated to the calls of the resident killer whales that they hear frequently without ever associating them with an attack. If associative learning was the main behavioural mechanism in shaping the predator image (*i.e.* if seals generally do not respond to the calls of killer whales but have learned to associate the calls of transients with a predatory threat) the seals would not have reacted to the unfamiliar calls. Since they have no experience with the calls of Alaskan killer whales there is no opportunity for associative learning to occur. Note that one cannot infer why the harbour seals responded to the calls of transient killer whales. Either they could have associated these calls with a predatory threat or, because transient killer whales vocalise only infrequently, seals may not have had the opportunity to habituate to these calls. Investigating the seals' response to the playback of sounds of harmless marine mammal species (e.g. humpback whales *Megaptera novaeangliae*) would be useful here.

As mentioned before, having an imprecise predator image generates fitness costs. Having a predator image that is too general and thus includes harmless stimuli leads to a waste of locomotory energy, as well as lost opportunities to forage and to reproduce. On the other hand, a predator image that is too specific will fail to include certain dangerous stimuli. It is important to note that the currencies of cost for the two types of imprecision are not equal: an individual with a predator image that is too general risks losing a meal (or a mating opportunity or wasting energy) whereas an individual with an over-specific predator image risks its life. When animals are limited in their ability to discriminate between harmless and dangerous stimuli (as all animals are to some extent), they cannot at the same time maximise the probability of correct detection of predators while minimising the probability of a false alarm (Wiley 1994). Since the results of losing a life are far more consequential than the results of missing a meal or a mating opportunity, one would expect animals to maximise the probability of correct detection of predators at the expense of an increase in false alarms. This means that animals should generally have a predator image that is too general rather than too specific. If an animal adjusted its predator image by associative learning alone, it would initially have a predator image that is too specific and would only arrive at a predator image that reflected the actual predatory threat by adding stimuli through associative learning (either by being attacked or by seeing conspecifics responding to a certain stimulus, e.g., Curio 1993). To incorporate a novel predatory stimulus, this associative learning therefore requires experience with the predator, which is extremely risky. On the other hand, starting out with a general predator image and adjusting it by selective habituation to reflect the actual predatory threat will confer costs from false alarms but not from missed detections of predators. It does not require experience with the predator, since any novel stimulus that falls within a certain predator class will elicit a response. By adjusting their responses to killer whale calls through selective habituation to harmless stimuli harbour seals therefore pursue the more conservative and therefore advantageous strategy.

CHAPTER V - Variation in the Vocal Repertoires of Transient Killer Whales

1 INTRODUCTION

1.1 Correlates and Function of Vocal Variation in Birds and Mammals

Repertoire variation describes differences in the sets of vocal patterns produced by different individuals, social groups, or populations. Such differences in vocal repertoires are a common phenomenon in many songbirds, but have also been documented in several taxonomic groups of mammals. In songbirds and other territorial species, repertoire variation is often geographic, that is, neighbouring individuals will have many song elements in common, whereas individuals from more distant territories share only few elements (*e.g.*, Mundinger 1982; Payne 1996). Such geographic variation in vocal repertoires is often primarily a by-product of the learning process, since juveniles match their repertoires to those of individuals nearby through vocal learning. Often however, the resulting vocal variation does have functional significance since individuals may use vocal cues to distinguish between territorial neighbours or intruders (e.g., Brooks & Falls 1975; McGregor & Avery 1986). Similarly in several species of mammals, individual variation in the vocal behaviour is used to make inferences about the social identity of callers (*e.g.*, McComb *et al.* 1993; Holekamp *et al.* 1999; McComb *et al.* 2000).

In group-living animals, members of social groups often match their vocal patterns, so that vocal variation yields information about the group identity of a vocalising individual rather than just individual identity or geographic provenance. Group-specific dialect variation has been shown in many group living birds (e.g., Trainer 1989; Wright 1996; Bartlett & Slater 1999), but also in bats (*e.g.*, Boughman 1997) and some cetaceans (*e.g.*, Ford 1991; Weilgart & Whitehead 1997; Rendell & Whitehead in press). Playback experiments to parrots (Wanker *et al.* 1998) and bats (Boughman & Wilkinson 1998) have shown that group-specific vocal variation is used in the recognition of group members and therefore has functional significance in these animals and is not merely a by-product of the learning process.

1.2 Variation in the Vocal Repertoires of Killer Whales

That repertoires of stereotyped calls of killer whales show geographic variation between distant locations has been known for some time (Awbrey *et al.* 1982). However, the full complexity of vocal variation among social groups of killer whales has only been demonstrated by the research of Ford (1989; 1991) on the vocal dialects of two populations of fish-eating killer whales in the northeastern Pacific, called the northern and southern resident community. Ford (1989) distinguished between three kinds of pulsed calls according to their degree of stereotypy. Discrete calls are highly stereotyped and can easily be assigned to different call types according to their structural properties. 70 to 95% of pulsed calls fall into this category. Variable calls are not repetitive and cannot be divided into clearly defined call types. Finally, aberrant calls are structurally based on a discrete call type, but show some degree of modification. Like whistles, these tend to occur most frequently during social interactions (Ford 1989).

Ford (1991) showed that different matrilineal social groups of resident killer whales produce group-specific repertoires of 7-17 call types of discrete calls. Whereas the structure of some call types experiences subtle modification with time (Deecke *et al.* 2000), the repertoire of call types produced by a given group remains stable over long periods of time (Ford 1991). Matrilineal groups which are presumably related may share some of these stereotyped call types, however, they often produce structurally distinct variants of these shared call types (Ford 1989; Deecke *et al.* 1999; Miller & Bain 2000). However, some matrilines within the same population do not have any call types in common in spite of frequent social contact (Bigg *et al.* 1990; Ford 1991). The northern resident population of killer whales inhabits the waters off central and northern British Columbia and is divided into three acoustic clans, a clan being defined as a group of matrilines that share at least one call type (Bigg *et al.* 1990; Ford 1991). In total, Ford (1991) recorded 44 different call types and subtypes from northern resident killer whales. Similar patterns of vocal variation have since been described from fish-eating killer whales from Norwegian (Strager 1995) and Alaskan (Yurk *et al.* 2002) waters.

Transient killer whales inhabit the same waters as fish-eating residents, but feed exclusively on marine mammals and occasionally sea birds (Ford *et al.* 1998). Resident and transient killer whales show striking differences in many aspects of their behaviour and social organisation (Bigg 1982; Bigg *et al.* 1990). For this reason, it does not appear justified to assume that similar patterns of repertoire variation exist among transient killer whales. Two studies have investigated repertoire variation among mammal-hunting killer whales and both were conducted in the northeastern Pacific. Using a sample of 10 recordings of seven social groups of West Coast transients, Ford (1984) and Ford & Morton (1991) established a vocal repertoire of eight call types, none of which were produced by the sympatric fish-eating populations. Saulitis (1993) studied the vocal behaviour of a small and apparently isolated group of 22 transient killer whales from Prince William Sound, Alaska. She categorised the vocal repertoire of this group into 13 discrete call types, none of which matched call types of the West Coast transient population. It is unclear whether this apparent difference in repertoire size reflects true differences in the complexity of the vocal repertoire or is due to the different criteria used for call categorisation in the two studies.

1.3 Objectives

Since the studies of Ford (1984) and Ford & Morton (1991), we have gained much new information about the behaviour, movement patterns and social structure of the West Coast transient population. The known size of this population has expanded from 49 identified individuals in 1982 (Ford & Fisher 1982) to over 200 individuals in 1999 (Ford & Ellis 1999). We know that the West Coast transients form a continuous population that ranges from Monterey Bay, California to Glacier Bay in Southeast Alaska. The western boundary of the population's range, however, remains unclear. Whereas certain members of the population have only been seen in a subsection of the population's range, others have been seen along the entire coast from California to Southeast Alaska (*e.g.*, Goley & Straley 1994). In addition, the number of recordings of transient killer whales from different parts of their range has increased vastly in recent years.

In this chapter, I reassess the vocal repertoire of transient killer whales using the methodology outlined in Chapter II. I test whether vocal repertoires of transient killer whales vary between different social groups or between regions within the population's range. Finally, I compare the complexity of repertoire variation in resident and transient killer whales to see if variation is comparable between the sympatric ecotypes.

2 METHODS

2.1 Recordings of Transient Killer Whales

For this study, I analysed a database of 66 recordings of transient killer whales made between 1970 until 2002. This database was compiled by John K.B. Ford and was supplemented with my own recordings obtained in four field seasons from 1999 to 2002. Recordings were contributed by various researchers using a variety of recording systems. Most systems had approximately flat frequency responses between 100 Hz and 10 kHz. Details on the recordings are given in Appendix II. The amount of information available for each recording session varied: the general locations of the encounters were available for all recording sessions. For 50 recording sessions, all individuals in the group had been identified photographically, for nine recordings only some members were photographed and in seven recordings, no information on the identity of the recorded animals was available. 41 of the recordings were made in the waters off

British Columbia, Canada, 20 in Southeast Alaska, USA between the British Columbian border and Glacier Bay, and five came from central California, USA (primarily Monterey Bay).

2.2 Acoustic Analysis

The recordings of transient killer whales were digitised at 44.1 kHz and individual calls were extracted using the CoolEdit 2000 acoustic analysis package (Syntrillium Software). Using a customised sound analysis program written in MATLAB (The MathWorks Inc.), spectrograms were generated from the sound files using an FFT length of 2048 points, a frame length of 1024 points and an overlap of 87.5% between frames. This resulted in a frequency resolution of 21.533 Hz and a time resolution of 2.902 ms. The quality of each call was rated from the spectrogram on a scale from one (lowest) to five (highest) taking into account signal-to-noise ratios, echoes, reverberations, and background noise. Spectrograms were inspected visually and calls were assigned to one of the call types defined by Ford & Morton (1991) whenever possible. Frequency contours were extracted from the spectrograms using the method described by Deecke *et al.* (1999), but the length of contours was not standardised for this analysis. In order to reduce computing time in the subsequent analyses, the time resolution of frequency contours was reduced to 10 ms by linear interpolation.

2.3 Automated Categorisation and Classification of Calls

In order to avoid artefacts such as background noise or missed sections of the calls from influencing the automated categorisation, only frequency contours of calls with the two highest quality scores were used to categorise the vocal repertoire. The automated categorisation method described in Chapter II, combining dynamic time-warping and an ART2 neural network, was used to divide the sample of calls into individual call types. The vigilance parameter, which determines the level of similarity required to assign a certain frequency contour to one of the reference patterns, was set to 81.24%. In a previous experiment (see Chapter II), this value yielded the highest ratio of within- and between-category variation and therefore explained a maximum amount of call variation with a minimum number of categories. In order to avoid establishing call types for calls that were not stereotyped (*i.e.* variable or aberrant calls of Ford, 1989), call categories that contained calls from only a single recording session were removed from the analysis. Consistent with previous naming systems for killer whale call types (*e.g.*, Ford 1987; Saulitis 1993; Strager 1995), call types were named with the population identifier WCT (for West Coast transients) followed by a two digit number. Where call types were largely consistent with those established by Ford (1984) and Ford & Morton (1991), the corresponding numbers were retained.

The reference contours generated in the categorisation were then used to classify all calls belonging to the three highest quality categories where each frequency contour was assigned to the call type represented by the reference contour it was most similar to. Including an additional quality category after call categories were established ensured a maximum use of data without risking establishing call categories due to artefacts resulting from poor acoustic quality. To identify variable and aberrant calls, I modelled the distribution of similarity values for all contours belonging to a given category and the reference contour for this category with a Weibull distribution (Devore 2000). Calls with similarities above the lower 90% confidence limit of the distribution were classified as discrete calls. Calls with similarity values between the 90 and 95% limit were classified as aberrant and calls whose similarity was below the 95% confidence limit were classified as variable calls and not assigned to any call type.

2.4 Comparison of Vocal Repertoires

In order to determine to what extent vocal repertoires differed between social groups of transient killer whales, I plotted the frequency distribution of the different call types for all recordings from which 50 or more calls with a quality rating of three or higher were available. Limiting this analysis to recording sessions with many calls would exclude recordings where only a small proportion of the vocal repertoire of the group present was recorded. In order to test for regional variation in the vocal repertoire between different parts of the range of the West Coast transient population, I assigned all recordings to one of three regions (California, British Columbia, and Southeast Alaska) and determined which call types had been recorded in the different regions. A call type was considered present in a region if it had been recorded at least once there.

3 RESULTS

3.1 Acoustic Analysis

A total of 5140 pulsed calls were digitised from the 66 recordings of transient killer whales. Of these, 24 calls (0.5%) had a quality rating of five and 568 calls (11%) a quality rating of four and were therefore used in the categorisation to establish call types. An additional 1273 calls (25%) had a quality rating of three and were included to determine vocal repertoires. 3274 (64%) calls had quality ratings of one and two and were omitted from the analysis. Of the 592 calls used to establish call types, 236 (40%) came from California, 280 (47%) from British Columbia, and 76 (13%) from Alaska. Of the 1865 calls used to determine vocal repertoires, 674 (36%) came from California, 899 (48%) from British Columbia, and 292 (16%) came from Alaska. A total of 10 recording sessions (three from California, five from British Columbia, and two from Southeast Alaska) yielded 50 or more calls with quality ratings of three or higher.

3.2 Categorisation and Classification of Calls

The ARTwarp neural network required seven iterations to consistently assign the 592 calls in the training set to the same call category between iterations. At this point it had established 15 categories or call types. Of these, two call types consisted of calls from a single recording session (two calls in one case, one call in the other), and were therefore removed from the analysis. Table II shows the proportion of calls assigned to the different call types and the degree of consistency with the call categorisation of Ford (1984) and Ford & Morton (1991). Representative spectrograms for the different call types are given in Appendix III.

Table II: Frequency of occurrence of the different call types of West Coast transient killer whales and degree of overlap with the classification system of Ford & Morton (1991). For each call type, figures in bold indicate the call type of maximum overlap of Ford & Morton (1991).

Call Type	**Number of calls matching to call type of Ford & Morton (1991)**								**Number (percent) of calls**
	T01	T02	T03	T07	T08	T09	T10	variable aberrant	
WCT01	**498**	-	-	-	-	-	-	1	499 (26.8%)
WCT02	1	**263**	-	-	3	-	-	3	270 (14.5%)
WCT03	-	2	**83**	33	-	1	-	3	122 (6.5%)
WCT04	-	-	**17**[1]	-	-	-	-	-	17 (0.9%)
WCT07	-	-	10	**115**	-	-	-	3	128 (6.9%)
WCT08	-	-	-	-	**194**	-	-	1	195 (10.5%)
WCT09	-	-	-	-	-	**27**	-	1	28 (1.5%)
WCT10	-	-	-	-	-	1	**43**	-	44 (2.4%)
WCT11	**285**	-	-	-	-	-	-	3	288 (15.4%)
WCT12	-	-	4	**62**[2]	-	-	-	9	75 (4.0%)
WCT13	-	-	**14**	10	-	-	-	11	35 (1.9%)
WCT14	-	-	-	-	-	**39**	12	-	51 (2.7%)
WCT15	-	-	-	-	**15**[3]	-	-	-	15 (0.8%)
aberrant	20	3	1	2	2	1	3	15	47 (2.5%)
variable	25	3	1	3	1	-	-	18	51 (2.7%)
Number (percent) of calls	829 (44.5%)	271 (14.5%)	130 (7.0%)	225 (12.1%)	215 (11.5%)	69 (3.7%)	58 (3.1%)	68 (3.6%)	1865 (100%)

[1] Call type T04 of Ford (1984), and subtype T03iii of Ford & Morton (1991).
[2] Subtype T07ii of Ford & Morton (1991).
[3] Subtype T08ii of Ford & Morton (1991).

In general, call categorisation by the neural network created somewhat finer categories than those established by Ford (1984) and Ford & Morton (1991). This means that several of their call types were divided into two in the current analysis (often consistent with subtypes of Ford & Morton, 1991). Nevertheless, the overlap with the categorisation of Ford & Morton (1991) is extensive: call type T01 was divided into call type WCT01 and WCT11, call type T02 is identical to call type WCT02, T08 was divided into call types WCT08 and WCT15 with the split being consistent with the division between subtypes T08i and T08ii of Ford & Morton (1991). Call type T09 of Ford & Morton (1991) was divided into the call types WCT09 and WCT14 by the current analysis and call type T10 is largely consistent with call type WCT10. The main discrepancies are call types T07 and T03 of Ford & Morton (1991), calls of which were assigned to call types WCT03, WCT04 (subtype T03iii of Ford & Morton, 1991), WCT07, WCT12, and WCT13.

3.3 Variation in Vocal Repertoires

The dates, locations and individuals present for the 10 recordings with 50 or more calls of good acoustic quality are given in Table III. The frequency distributions of different call types from these recordings are shown in Figures 13 and 14. Repertoire sizes ranged from four (95-05-15) to 10 call types (87-10-08 and 92-05-02) with a median of seven call types. However, due to the relatively small numbers of calls, vocal repertoires shown are not necessarily comprehensive. Looking at these recordings it becomes clear that the vocal repertoires of West Coast transient killer whales show comparatively little variation: of the 13 call types, three (WCT01, WCT02, and WCT11) occurred in all 10 recordings, and another one (WCT08) occurred in all but one. Of the remaining calls, two (WCT03 and WCT07) occurred in six recordings and one (WCT13) in four recordings. Call

Table III: Group membership and location for recordings of West Coast Transients from California, British Columbia, and Southeast Alaska. Only recordings with 50 calls or more are listed.

Recording Date (yy-mm-dd)	**Location**	**Recorded by**	**Individuals present**[2]	**No. of calls**[1]
California				
87-10-08	Monterey Bay	N. Black	N/A	111
92-05-02	Monterey Bay	P.D. Goley	T132, T134, T135 + at least 14 others	365
99-05-00[3]	Monterey Bay	R. Ternullo	N/A	192
British Columbia				
70-05-05	Pedder Bay	P. Spong	T001, T002 + possibly others	179
80-08-12	Deserter Islands	J.K.B. Ford	T034, T035, T036, T037, T038	103
95-05-15	Laskeek Bay	R. Burke	T040, T070, T071, T071A, T086, T086A, T118, (T121)[4]	64
99-01-04	Hardy Bay	J. Borrowman	T011, T011A, T012, T012A	97
02-08-22	Gordon Channel	V.B. Deecke	T018, T019, T019B, T019C, T142, T143	104
Southeast Alaska				
01-06-27	Tracey Arm	V.B. Deecke	T087, T088, T090, T090A, T101A, T102, T124, T124A, T124A1, T124A2, T124B, T124B1, T124C, T124D, T124E	174
01-06-28	Endicott Arm	V.B. Deecke	T090, T090A, T124, T124A, T124A1, T124A2, T124A2, T124B, T124B1, T124C, T124D, T124E	50

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[1] Number of calls with a quality rating of three or higher (see Methods of Chapters II and Chapter V for details).

[2] Identification names according to Ford & Ellis (1999).

[3] Day not known.

[4] Identification names in brackets refer to animals that could not be identified unequivocally from the photographs.

types WCT10, WCT09, WCT12, and WCT15 each occurred in three of the 10 recording sessions. Call type WCT14 occurred in two recording sessions (both from California) and WCT04 in a single recording session from British Columbia (however, this call type also showed up in two recording sessions with less than 50 calls from Southeast Alaska). Most recordings also included aberrant and variable calls (aberrant: nine out of 10 recordings, variable: eight out of 10 recordings).

A comparison of vocal repertoires between California, British Columbia and Southeast Alaska (Table IV) shows differences in the vocal repertoires recorded in different parts of the range of the West Coast transient population. A large proportion (five of 13) of call types occurred in all three regions. Two call types (WCT04 and WCT07) were recorded in British Columbia and Southeast Alaska, but not in California and one (WCT15) occurred in California and in a single recording session from British Columbia, but not in Alaska. Four call types (WCT09, WCT10, WCT12, and WCT14) were only recorded in California. No call types were unique to recordings from British Columbia or from Southeast Alaska.

Table IV: Geographic differences in the vocal repertoires of West Coast transients between California, British Columbia, and Southeast Alaska. X indicates that a certain call type was recorded in the region.

Region	Call Type													Number of calls
	WCT 01	WCT 02	WCT 03	WCT 04	WCT 07	WCT 08	WCT 09	WCT 10	WCT 11	WCT 12	WCT 13	WCT 14	WCT 15	
California	x	x	-	-	-	x	x	x	x	x	x	x	x	674
British Columbia	x	x	x	x	x	x	-	-	x	-	x	-	x	899
Southeast Alaska	x	x	x	x	x	x	-	-	x	-	x	-	-	292

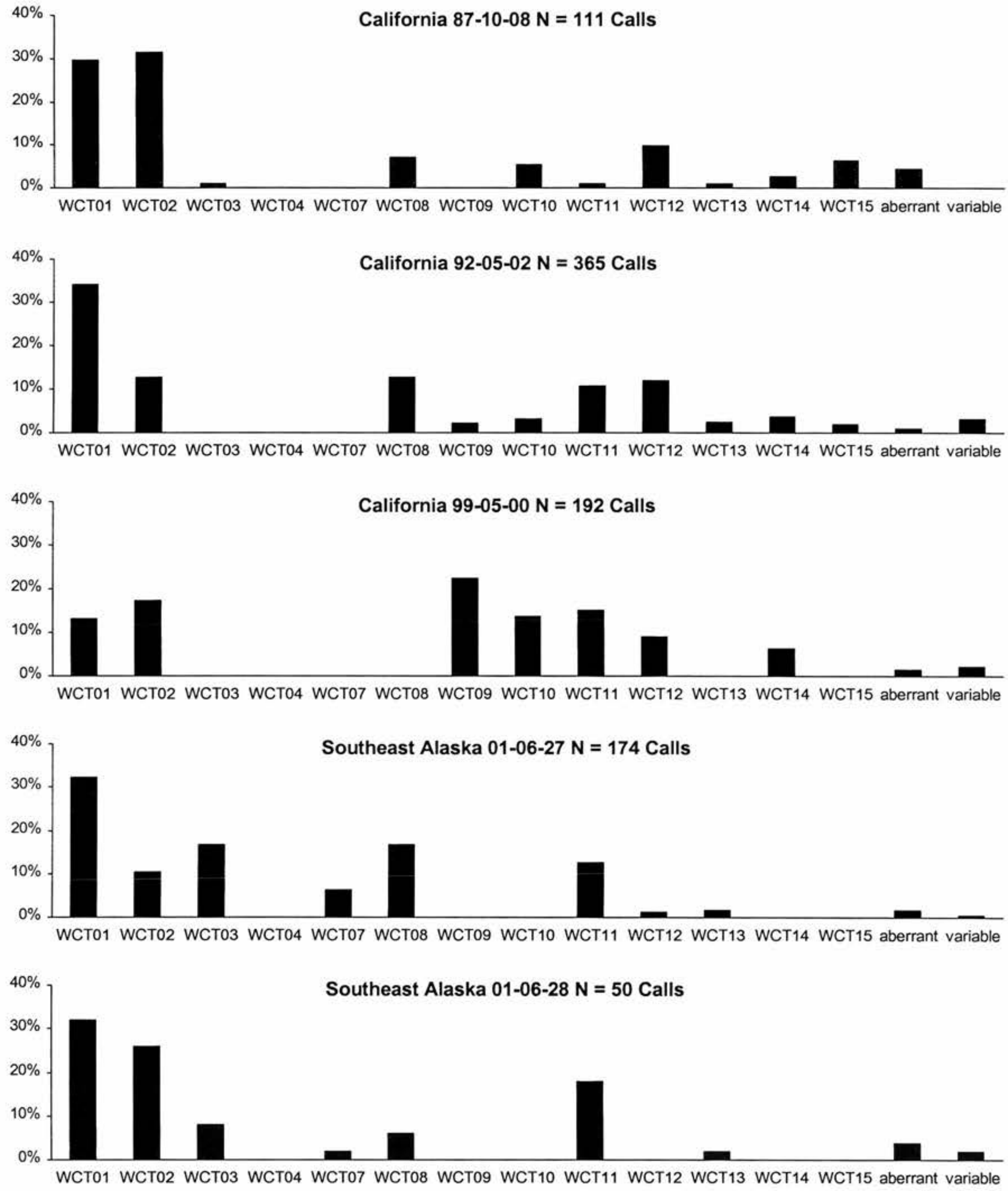

Figure 13: Vocal repertoires and frequency of call use among West Coast transients from California (top three panels) and Southeast Alaska (bottom two panels). Only recordings yielding 50 or more calls of good quality are shown.

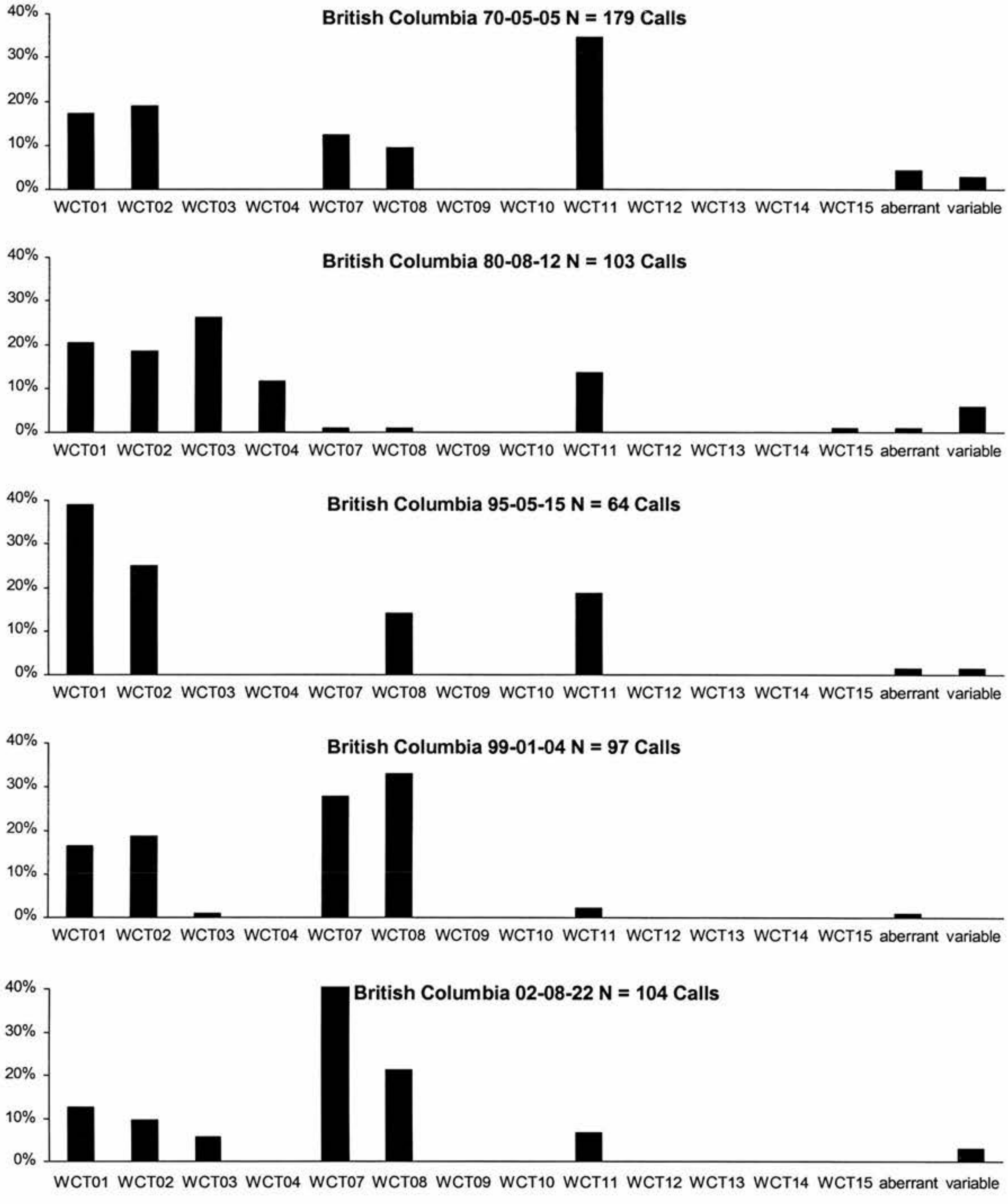

Figure 14: Vocal repertoires and frequency of call use among West Coast transients from British Columbia. Only recordings yielding 50 or more calls of good quality are shown.

4 DISCUSSION

4.1 Syntax Rules in West Coast Transient Killer Whales

Ford (1984; 1989) noticed that some discrete calls of resident and transient killer whales are governed by a strict syntax rules: among the northern resident killer whales the call types BCN07 and BCN08 frequently occur together. Whereas a BCN07 call is not always followed by a BC08 call type, the BC08 call type is never produced without an introductory BC07. Ford & Morton (1991) noticed a similar relationship between their call types T01 and T02. A preliminary analysis of such syntax rules appears to confirm the validity of some of the calls types established by the current analysis. While call types WCT01 and WCT11 may appear similar in structure, the WCT01 call type is often followed by a WCT02 call type, but never by WCT08. WCT11 in contrast is often followed by a WCT08 call (or a WCT14 or WCT15 call in California), but never by a WCT02. WCT08 often follows an introductory WCT11, and WCT02 always follows WCT01 or, in California, WCT10. Such syntax rules also govern the structurally similar call types WCT09, WCT10, and WCT14: WCT09 is always preceded by a WCT11. WCT10 is produced alone or followed by a WCT02 call, and WCT14 is usually produced alone. While further research is required to establish the validity and to examine the function of these syntax rules, the fact that many call types that appear superficially similar but were divided by the automated categorisation appear to be governed by different rules of syntax suggests that the analysis does categorise the structural variation of stereotyped calls in a way that appears to be biologically meaningful.

4.2 Patterns and Extent of Variation in the Vocal Repertoire

The analysis of geographic variation in the repertoires of West Coast transients shows that most of the repertoire differences occur between California on the one hand and British Columbia and Southeast Alaska on the other. Three (27%) of the 11 call types recorded in California are not found in other parts of the population's range. By comparison, transients recorded in British Columbia and Southeast Alaska have almost identical vocal repertoires: Only one (10%) of 10 call types recorded in British Columbia does not appear to occur in Alaska (this call type occurred in only one recording from British Columbia). The vocal distinctness of transient killer whales from California coincides with differences in their ecology. The coasts of British Columbia and Southeast Alaska provide a very similar habitat of sheltered fjords and inlets with a very similar abundance of prey species (the main difference being the presence of tidal glaciers in Alaska, which provide pupping habitat for harbour seals on the ice floes). By contrast, the California coast is far more exposed offering only few bays and inlets so that it constitutes a very different habitat. Whereas transient killer whales have been seen attacking baleen whales only on a few occasions in British Columbia and Southeast Alaska (Baird & Dill 1995; Ford *et al.* 1998), such attacks are commonly reported from the California coast (*e.g.*, Baldridge 1972; Jefferson *et al.* 1991; Goley & Straley 1994) and three of the five recordings of transient killer whales analysed in this study were made during attacks on grey whales.

The hunting strategies required to overcome large prey such as grey whales in open water are probably quite different from those used to hunt small cetaceans or pinnipeds in the enclosed bays or inlets of British Columbia or Alaska.

When attacking grey whales, transient killer whales usually focus on calves and work in groups of three to 17 individuals. Attacks tend to involve a high degree of cooperation between individual killer whales (Jefferson *et al.* 1991; Goley & Straley 1994). A striking difference in hunting strategy is that these killer whales are often vocal during the attack (P.D. Goley, *pers. comm.*, R. Ternullo, *pers. comm*) while transients in British Columbia and Southeast Alaska usually only start vocalizing once the prey is dead (see Chapter III). The differences in the vocal repertoire of transient killer whales in California and further north are therefore consistent with ecological differences between the two regions. However, it remains unclear to what extent the repertoire differences represent individual or group-specific variation, or are linked to the different behavioural context involved in cooperatively hunting large whales. A comparison of recordings involving the same individuals made in California and further north, as well as an analysis of recordings made during the attack on baleen whales in British Columbia or in Alaska would help to answer this question.

4.3 Comparison with Resident Killer Whales

With between four and 10 call types per group and between nine and 11 call types per region, the vocal repertoires determined in this study are small in size compared to those of resident killer whales. Ford (1991) mentions that resident pods produced 7-17 (mean 10.7) call types; it is important to bear in mind that the current analysis generated somewhat finer categories than those of Ford (1991). Yurk *et al.* (2002) found an average repertoire size of 12 call types among pods of resident killer whales in Alaska. At the level of the population the difference in vocal repertoires is even more striking: while the current study identified only 13 call types in the West Coast transient population (population size: more than 219 individuals in 1998, Ford & Ellis 1999), Ford (1991) identified a total of 44 call types and subtypes from the similarly sized Northern resident population (population size: approximately 216 individuals in 1998; Ford *et al.* 2000). Yurk *et al.* (2002 report a population repertoire of 39 call types and subtypes from Alaskan resident killer whales (population size: 115 individuals in 1998; Matkin *et al.* 1999).

Not only the size of vocal repertoires but also the amount of sharing of call types differs between resident and transient killer whales. Ford (1991) grouped all resident social groups that shared at least one call type into a common acoustic clan. He found that the northern resident population of killer whales contained three acoustic clans, whereas the southern resident population (population size: 83 in 1999; Ford *et al.* 2000) was comprised of a single acoustic clan. Yurk *et al.* (2002) found that the Alaskan resident population consisted of at least two acoustic clans. This means that many individuals within a resident population share no call types at all, even though they frequently interact. Within a resident population, individuals in the same acoustic clan share between 30 and 100% of their vocal repertoire (Ford 1991; Yurk *et al.* 2002). In the current study three call types (23%) appear to be shared by all members of the West Coast transient population, and one additional call type may also be universal (the WCT08 call type occurred in all but one recording with 50 or more calls and its absence in the one recording may be due to small sample size). This suggests that the vocal variation found within the entire population of West Coast transient killer whales is comparable to that found within a single resident clan.

4.4 Causal and Functional Explanations for Differences in Repertoire Variation

Several non-exclusive aspects of the social organisation and population genetics of resident and transient killer whales can account for the observed differences in the amount of repertoire variation between them. In situations where vocal patterns are learned, variations in vocal repertoires are the direct results of selectivity during the learning process. Such selectivity arises when an individual does not copy all vocal patterns in the population because it only ever experiences a subset of vocal patterns or because it actively chooses not to copy certain patterns (Lynch 1996). Causal explanations for the observed differences in vocal variation therefore must focus on differences in the patterns of contact and exchange between individuals in the different populations of killer whales. There are indeed striking differences in these variables between resident and transient killer whales: the matrilines of resident killer whales represent closed social groups with no permanent emigration from or immigration into the group (Bigg *et al.* 1990). While the members of a matriline have extensive contact with members of other matrilines when these social groups join and travel together for extended periods of time, they spend their entire lives in close social interaction with a stable set of social companions. By contrast there is evidence for permanent dispersal in transients of both male and female offspring from the maternal group (Ford & Ellis 1999; Baird & Whitehead 2000). This exchange of individuals between social groups could explain the greater degree of sharing of vocal patterns observed in the transient population.

As shown in Chapter III, resident and transient killer whales show striking differences in the frequency of occurrence of vocal behaviour and this difference may play a role in generating the observed differences in the amount of repertoire variation. If modifications to vocal patterns arise only from errors made during their production (*e.g.*, Lynch 1996), it may be the case that vocalisations remain more stable if they are produced less frequently. However, the lower level of vocal activity of transient killer whales also means that any individual in the transient population will have less experience with vocalisations of other members of the population, which in turn would decrease the opportunity for copying and thus vocal matching, as well as its precision. The effects of the reduced levels of vocal activity among transient killer whales on the amount of vocal variation therefore remains unclear and should be addressed in future studies. Determining the rate of structural modification experienced by call types of transient killer whales using the methodology of Deecke *et al.* (2000) can help to resolve this issue.

Recent analyses of the genetic variation of killer whales in the Northeastern Pacific have revealed striking differences in the amount of genetic variation found within resident and transient populations. Using microsatellite markers, both Hoelzel *et al.* (1998) and Barrett-Lennard (2000) found significantly lower levels of heterozygosity among residents compared to transients. This finding would be expected if effective population sizes of resident populations are smaller that those of transients (Barrett-Lennard 2000). Effective population size has two important functional implications for the extent of repertoire variation. Reduced variation in the vocalisations could be advantageous in large populations that range over a large area, since it will allow different individuals to recognise each other as members of the same population, even though they encounter each other only rarely. Shared vocal patterns could serve as a badge for the identification of appropriate partners for cooperative hunting, mating, and social interactions.

Barrett-Lennard (2000) has shown that resident killer whales exhibit negative assortative mating by dialect: individual residents tend to mate with others that have very different call repertoires. The repertoire variation of resident killer whales represents an effective indicator of maternal relatedness (Barrett-Lennard 2000), probably because call repertoires are passed on along maternal lines. Effective population sizes of resident killer whales in the Northeastern Pacific are small (around 70 individuals; Barrett-Lennard 2000). Inbreeding is therefore a potential problem that could be aggravated by the lack of permanent dispersal within resident populations. Being able to identify even distant relatives in order to avoid mating with them could therefore bring substantial selective advantages to resident killer whales. If inbreeding indeed generates substantial fitness costs in resident killer whales, it could have led to the evolution of a dialect system where vocal repertoires change at a critical rate so that individuals are able to recognise mating partners that ensure an optimal level of outbreeding. Note that rates of repertoire change both higher and lower than this critical rate would not allow identification of adequate mating partners. If the rate of change is too low, even unrelated individuals would share vocal patterns, if the rate is too high, even close relatives would sound very distinct and in both cases the discrimination between adequate and inadequate mating partners is not possible.

Microsatellite markers show that gene diversity is significantly higher in transients (Barrett-Lennard 2000) compared to resident killer whales. This finding could imply a larger effective population size of West Coast transients compared to resident populations. In addition this could mean that this transient population is not closed as resident populations appear to be but receives limited gene flow from other killer whale populations in the Northeastern Pacific. Combined with the evidence for permanent dispersal of individuals from the natal group in transient killer whales, this suggests that inbreeding may not be as great as a problem among transients as it is for resident killer whales. For this reason, transient killer whales may not need to rely on acoustic cues to avoid inbreeding and can thus exhibit a lower rate of change of the vocal repertoire. If this indeed is true, the hypervariability of vocal repertoires has evolved in resident killer whales as a means of providing a precise indicator of genetic relatedness for the avoidance of inbreeding. Determining and comparing the genetic and acoustic diversity of killer whale populations world wide will help to address this issue.

CHAPTER VI - General Discussion

1 Summary

This study set out to investigate the vocal behaviour of a population of killer whales in the northeastern Pacific whose members specialise in hunting marine mammals, and to compare the behavioural context and frequency of occurrence of vocal communication, as well as the structure and variation in vocal patterns, to the communication system of the fish-eating killer whales that inhabit the same waters. Taking into account the extensive literature on the vocal behaviour of fish-eating killer whales, this study has identified important differences in the vocal communication of the two killer whale ecotypes. Perhaps the most striking is the difference in the frequency of occurrence of vocal behaviour. Fish-eating killer whales live in an acoustic environment that is dominated by underwater communication: they frequently produce pulsed calls, and vocal behaviour is associated with all behavioural contexts, including rest (Ford 1989; Ford 1991). Mammal-eating killer whales by contrast spend the majority of their lives in silence. Vocal communication is rare and occurs only in a few narrowly defined contexts.

The strong and consistent response of harbour seals to the playback of calls of transient killer whales provides some of the first experimental evidence that transient killer whales experience a large indirect cost for vocal behaviour, which in turn may explain why they vocalise so infrequently. This cost stems from the acute underwater hearing of harbour seals paired with their ability to learn to recognise sound patterns, abilities that are probably also found in many of the other marine mammal species that fall prey to transient killer whales. The pronounced difference in the response of seals to calls of familiar and unfamiliar killer whales illustrates the great extent to which these animals are able to discriminate between sound patterns. This finding suggests that, in a situation where the cues associated with the predator are highly variable and change with time, a response that can be modified by learning and experience offers superior protection.

The second difference between the acoustic communication of fish-eating and mammal-eating killer whales lies in the amount of structural variation found in the vocal patterns produced by different members of the same population. The vocal communication of resident killer whales is characterised by a great diversity in vocal patterns, and many members of the same population that frequently interact socially nevertheless have no part of their call repertoire in common. Transient killer whales, on the other hand, exhibit great conformity in their vocal patterns. We currently know little about the movement patterns of individual transient killer whales. However, since some groups have only been seen in a small part of the population's range, it seems likely that some individuals only encounter each other infrequently, or not at all. Yet, even these animals have a large proportion of their vocal repertoires in common. Although the cause for this difference in vocal variation has yet to be determined, the differences in social structure and effective population size between resident and transient killer whales provide a basis for interesting hypotheses about the causes and possible functions of repertoire variation in this species.

2 Prey Hearing and Dietary Specialisation in Killer Whales

Ford *et al.* (1998) suggest that the two forms of killer whales are the product of individual dietary preferences that were passed on from generation to generation through learning and ultimately became fixed in the population leading to dietary specialisation. Guinet & Bouvier (1995) provide some evidence for the transmission of such behaviour traditions among killer whales in the Southern Ocean. While this mechanism can explain dietary specialisation, it does not explain why diets diverged along taxonomic lines, that is, why one population ultimately specialises on fish and the other on mammals. A divergence of diets along discontinuities in the distribution, or habitat preferences, of different prey species would seem more plausible, causing different killer whale populations to specialise on all potential prey animals that are available in a certain region or habitat. Baird *et al.* (1992) speculate that reproductive isolation may be the result of indirect trophic interactions between the two ecotypes (since resident killer whales potentially compete with the prey of transients).

Although the divergence between fish-eating and mammal-eating killer whales has been reported from other parts of the world (Berzin & Vladimirov 1983), this divergence does not appear to be universal: killer whale populations that feed on fish as well as marine mammals have been described from the Southern Ocean (Guinet 1992) and the waters around New Zealand (Constantine *et al.* 1998). However, in areas where dietary specialisation has occurred, the dietary preferences of individuals appear to be strong: while resident killer whales captured for display in aquaria readily accepted dead salmon, a group of transient killer whales captured in 1970 fasted for 79 days before accepting fish, by which time one of the animals had died, apparently of starvation. The remaining members of the group were subsequently released and immediately returned to feeding on marine mammals (Ford & Ellis 1999).

It appears that the different hearing abilities of fish and marine mammals may hold a clue as to why in some regions killer whales have diverged into distinct ecotypes, some of which specialise on hunting marine mammal while others hunt fish. Along with the research of Barrett-Lennard *et al.* (1996), the results of this study suggest that killer whales cannot employ a common hunting strategy to effectively hunt both fish and marine mammals at the same time. In order to maximise the capture of fish, the animals should rely on their echolocation to detect and capture their prey. However, this would be a poor strategy to capture acoustically sensitive prey, if stealth and surprise is required to overcome the prey's defences. Even in areas where killer whales appear to feed on fish as well as on marine mammals, foraging for the two prey types is spatially and temporally segregated (Guinet 1992). The high cost of vocal behaviour when hunting acoustically sensitive prey such as marine mammals can therefore explain why the dietary specialisation of killer whales in the northeastern Pacific and elsewhere follows strictly taxonomic (and not ecological or geographic) lines.

3 Neophobic Harbour Seals and Silent Killer Whales

The results of the playback experiments of killer whale calls to harbour seals raise an interesting question. While harbour seals responded strongly to any unfamiliar calls, the results show that they have habituated to the calls of fish-eating killer whales that they hear frequently and that are never followed by an attack. In Chapter III, I suggest that transient killer whales can probably not avoid detection by shifting their vocal communication to higher or lower acoustic frequencies. However, the fact that harbour seals have habituated to the calls of some harmless fish-eating killer whales suggests that increased vocal communication in transient killer whales could equally habituate harbour seals and other marine mammals to their calls, and thus effectively cancel the high ecological cost of vocal communication. Could desensitising the prey to the predator's vocalisations be an evolutionary strategy that allows predators to reap the benefits of acoustic communication without the associated ecological costs? Studies in the wild have shown that animals fail to habituate to the presence of predators even though they may encounter them frequently (summarised in Curio 1993). Even in situations where such habituation is possible (*e.g.*, in captive settings or the current study) dishabituation is usually instant and persistent if the predator-associated cue is ever paired with a real threat (or even if it elicits a strong response from a conspecific; Curio *et al.* 1978b).

If harbour seals and other marine mammals are less likely to respond to killer whales producing the familiar calls of the local fish-eating populations than they are to silent killer whales, one could argue that acoustic mimicry of the calls of local residents presents an effective behaviour strategy for transients to increase the chance of capture. However, the strong response of harbour seals to unfamiliar calls of fish-eating killer whales shows that the calls of residents initially fall into the class of predator-associated cues and are therefore probably subject to the same mechanism of rapid and persistent dishabituation if ever associated with an attack. It therefore appears that silence during the hunt is indeed the only stable behavioural strategy for mammal-eating killer whales.

4 Costly Calls and the Evolution of Cooperation

The term cooperation can be applied in a broad sense to situations where two or more individuals can achieve a common goal by coordinating their behaviour (*e.g.*, Goodall 1986; Jefferson *et al.* 1991). Hamilton (1964a;b) has defined cooperation more strictly and only applies the term to situations where an animal behaves in a way that will on average increase the long-term fitness of itself and one or more others, even if this entails a short-term decrease in its own fitness. Mutualism, kin-selection, and reciprocity may all contribute to this long-term fitness gain (Boesch & Boesch-Achermann 2000). One would expect cooperation to evolve in situations where the individual fitness gain of two or more animals coordinating their behaviour in the long term outweighs the gain of one animal acting alone.

By coordinating their movements and behaviours, two or more predators can often overcome larger prey or increase their probability of success (*e.g.*, Kruuk 1972; Schaller 1972; Boesch 1994). It has therefore been argued that the benefits of cooperative hunting could play a key role in the evolution of group living in carnivores and primates (*e.g.*, Schaller 1972; Hill 1982). However, some analyses of individual energy intake have shown that while group hunters have greater hunting success, especially for large prey, solitary hunters often have a higher individual energy intake (Packer *et al.* 1990; Caro 1994; but see Creel & Creel 1995). The role of cooperative hunting in the evolution of group living in predators therefore remains somewhat unclear.

The results of this study and those of Barrett-Lennard (1996) show that transients rarely emit pulsed calls and echolocation clicks while hunting. This suggests that stealth and surprise may be important elements of their hunting strategy, and requires behaviour to be coordinated since, in order to avoid detection, all members of a group must refrain from vocalising. A similar coordination of behaviour has been reported from chimpanzees (*Pan troglodytes*) when hunting monkeys in the Taï Forest where groups of chimpanzees usually coordinate their movements by vocalising and drumming on tree trunks. Such acoustic communication ceases completely once the chimpanzees hear the calls of monkeys (mainly *Colobus* and *Cercopithecus* spp.) in the forest canopy, and the chimpanzees are often able to avoid detection until they are beneath their intended prey (Boesch & Boesch 1989; Boesch & Boesch-Achermann 2000). Similar stealth and restriction of acoustic behaviour has been reported from Gombe, when groups of chimpanzees patrol territory borders or move inside the territory of a neighbouring community (Goodall 1986). Presumably this is to avoid detection by other potentially aggressive chimpanzees in the area, and individuals will often silently approach and threaten other group members (or human observers) who break the silence (Goodall 1986; R.W. Byrne *pers. comm.*).

In situations where group hunters attack acoustically sensitive prey by stealth, the costs and benefits of coordinating behaviours are shifted. In most other situations, one would expect group hunters that fail to coordinate their behaviours to have a capture success close to that of solitary hunters. This implies that, while there may be a benefit for coordinating behaviour, there is no additional cost for the lack of coordination (aside from the cost of group living, e.g., competition and interference). However, in a situation where stealth substantially increases the probability of a successful attack, lack of coordination of behaviour can carry a significant cost: if one individual in the group vocalises while the others hunt silently, the success of every individual in the group can potentially drop far below the success of an individual hunting alone. Where group living has evolved, the coordination of vocal behaviour is therefore the only stable strategy for predators hunting acoustically sensitive prey.

5 Further Research

Like most research this study has answered some questions but raised many more. I have investigated mechanisms responsible for fine-tuning the responses of animals to acoustic stimuli in their environment. Although the difference in the response of harbour seals to familiar and unfamiliar calls of resident killer whales shows that learning and experience play a role, further research is required to identify the mechanisms of learning involved. Employing time-depth recorders to investigate responses of different-aged individuals (rather than measuring group responses as in the current study) would help to identify how fast and when learning occurs. Consecutive playbacks of unfamiliar calls at the same haulout would also help to determine the amount of exposure required for habituation, as well as the strength and persistence of dishabituation, if the calls are subsequently paired with a negative stimulus. The role of cultural transmission should also be looked at: can witnessing the absence of escape responses in habituated conspecifics when hearing unfamiliar calls accelerate selective habituation in an individual? This question may best be answered in a captive or semi-captive setting. Finally, the behavioural measures used in the current study were too coarse to describe the nature of the anti-predator response in detail. Further studies should investigate what harbour seals do once they dive and when and where they return to the surface. Again, time-depth recorders, possibly combined with heart-rate monitors, will be useful here.

The low amount of vocal variation found in the genetically variable transient killer whale population documented in Chapter V, combined with the possible function of such variation in inbreeding avoidance (Barrett-Lennard 2000), could imply an inverse relationship between genetic and vocal variation among killer whale populations. Members of populations with low genetic variation pay great costs for mating with kin and this could have selected for faster rates of vocal change that allows for the refinement of acoustic recognition of relatives. A worldwide comparison of acoustic and genetic variation within populations of killer whales presents a first and useful step towards addressing this question, and information on genetic variation in killer whales is becoming available from many parts of the species' range (Barrett-Lennard 2000; Hoelzel *et al.* 2002). Such a study would have to be collaborative to benefit from the knowledge of local researchers. Historically an impediment to this kind of analysis has been the difficulty of determining the sizes of vocal repertoires and comparing them between studies. The methodology described in Chapter II provides a powerful tool enabling researchers to measure repertoire size and thus vocal variation as unambiguously as genetic variation can be determined from microsatellite markers.

In spite of the extensive research on the vocal communication of killer whales, we have obtained only a few glimpses into why killer whales produce pulsed calls at all. Ford (1991) and Yurk *et al.* (2002) showed that differences in vocal repertoires provide information about kinship among members of a population, and Barrett-Lennard (2000) found that individuals avoid mating with close kin, most likely basing their decisions on repertoire similarity. Schevill & Watkins (1966), as well as Miller (2000b) showed that killer whale calls contain information about the location and direction of movement of a calling whale and suggested that killer whales may be using this information to maintain contact with members of their group. However, many other questions about the adaptive significance of vocal communications in this species remain yet to be answered: are vocal signals primarily directed at other group members to coordinate behaviours within a group and to synchronise the behavioural states of its members, or do calls serve to establish contact with other groups in the area? Do vocal signals convey information about prey abundance or other information about the animals' environment? When it comes to these questions we are still very much in the dark.

Part of the difficulty of answering these questions is that vocal behaviour is so common in fish-eating killer whales: in residents, vocal behaviour can be recorded in all behavioural contexts, and for the few call types where associations with certain behaviours have been shown, these associations tend to be vague and by no means exclusive (Ford 1989). Transients present a very different situation: their vocal behaviour is limited to a few narrowly defined contexts, and further studies should examine possible associations of individual call types with certain behaviours. Because vocal behaviour carries a high cost in mammal-eating killer whales, transients should only call when the benefits for vocal communication are at least as high or higher. This will make it easier for researchers to identify what precisely these benefits may be. I would therefore argue that transient killer whales are an ideal study population for future research into the adaptive significance of vocal communication in *Orcinus orca*.

6 Conclusions

This study has compared the vocal communication of two forms of killer whales that are nearly identical in their morphology, their physiology of hearing and their sound production, and that share a common habitat and acoustic environment. Despite these similarities, the way that the two ecotypes use acoustic signals could hardly be more different. Resident killer whales live immersed in an acoustic world characterised by the calls of their fellow group members. Transient killer whales by contrast spend their lives in silence interrupted only rarely by brief bursts of vocal activity. Their repertoires of stereotyped calls are characterised by vocal conformity allowing the acoustic recognition of fellow members of the population over a large part of the North Pacific ocean basin. In contrast, vocal diversity is the defining feature of acoustic communication in resident killer whales and group-specific vocal repertoires exhibit an intricate system of variation that delineates maternal relatedness and thus potentially allows for precise recognition of degrees of kinship. While the findings presented in this thesis have shed light on the causes for some of the differences, others remain to be explained and this study has identified many paths down which further research can proceed. However, one single point is clear: systems of acoustic communication of animals are not static, but subject to modification by endogenous and environmental factors. Although such factor are often subtle, at times they lead to pronounced differences in the vocal communication of closely related groups. It is precisely these factors that have created and maintained the great diversity in the way acoustic communication manifests itself in the animal world.

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APPENDIX I: Responses of Harbour Seals to Playbacks at Different Seal Haulout Sites

Table A-I: Counts and distance measurements for the paired playback trials of transient calls and control sequences (Experiment 1).

Playback Sequence	Haulout[1]	Playback Type	Date	Number of seals at the surface			Distance to nearest seal (m)		
				before	after	change	before	after	change
70-05-05	H043	Treatment	07/09/00	19.5	7.3	-63%	33	51	53%
		Control	09/09/00	18.5	11.2	-39%	19	16	-17%
	H462	Treatment	26/09/00	5.2	1.8	-65%	83	111	34%
		Control	27/09/00	5.3	6.8	28%	62	69	11%
80-08-12	H027	Treatment	18/09/00	11.3	3.2	-72%	55	119	115%
		Control	17/09/00	10.7	10.8	1%	37	36	-2%
	H161	Treatment	27/09/00	9.3	7.5	-20%	57	68	18%
		Control	26/09/00	12.3	8.3	-32%	56	77	36%
95-05-15	H007	Treatment	01/10/00	10.7	8.2	-23%	89	74	-17%
		Control	30/09/00	13.7	12.2	-11%	35	58	66%
	H721	Treatment	13/06/01	8.5	2.3	-73%	101	91	-10%
		Control	12/06/01	7.3	7.2	-2%	80	85	6%
96-08-25	H028	Treatment	17/09/00	12.8	9.0	-30%	51	53	3%
		Control	18/09/00	17.0	18.5	9%	44	50	14%
	H009	Treatment	27/09/00	8.2	4.2	-49%	75	81	9%
		Control	28/09/00	7.7	6.7	-13%	82	82	0%

[1] see Olesiuk (1999) for locations of haulouts.

Table A-II: Counts and distance measurements for the playback trials of calls from different killer whale populations (Experiment 2).

Playback Type	Playback Sequence	Haulout[1]	Date	Number of seals at the surface			Distance to nearest seal (m)		
				before	after	change	before	after	change
Transient	70-05-05	H733	04/06/01	16.0	10.0	-38%	36	42	14%
		H062	03/09/01	21.3	17.2	-20%	50	73	32%
		H075	27/09/01	37.6	34.0	-10%	47	43	-8%
	80-08-12	H385	19/08/01	5.2	2.8	-45%	51	49	-4%
		H069	06/09/01	10.3	3.7	-64%	49	64	23%
	95-05-15	H729	06/11/01	9.7	3.2	-67%	95	110	14%
		H059	03/09/01	23.3	15.0	-36%	44	62	30%
		H005	29/09/01	11.6	6.2	-47%	93	96	3%
	96-08-25	H699	28/07/01	5.2	3.0	-42%	84	84	0%
		H243	04/09/01	5.7	1.7	-71%	73	59	-23%
BC-Resident	96-08-14	H726	06/07/01	9.0	9.5	6%	85	75	-14%
	81-07-12	H710	06/14/01	6.3	5.8	-8%	44	55	21%
	99-07-25	H404	29/07/01	13.7	8.0	-41%	94	92	-3%
	70-07-00	H074	06/09/01	8.8	7.8	-11%	84	93	10%
	73-10-29	H167	03/09/01	26.2	26.7	2%	56	60	6%
		H219	28/09/01	11.4	15.6	36%	62	53	-17%
	80-06-02	H531	04/09/01	17.0	20.2	19%	80	87	9%
		H016	28/09/01	9.6	9.3	-3%	40	32	-27%
	91-08-26	H067	05/09/01	11.2	9.2	-18%	42	44	5%
		H014	29/09/01	7.1	6.8	-4%	82	56	-47%
AK-Resident	84-09-18	H736	13/06/01	9.7	6.2	-36%	79	34	-137%
		H068	06/09/01	9.7	2.0	-79%	49	52	5%
		H004	28/09/01	23.0	16.7	-28%	38	45	16%
	90-07-15	H716	03/07/01	6.5	4.2	-36%	66	64	-4%
		H549	05/09/01	12.8	9.2	-28%	36	35	-1%
		H076	27/09/01	24.2	9.2	-62%	40	37	-8%
	97-07-23	H704	15/08/01	7.5	3.8	-49%	87	97	10%
		H073	06/09/01	15.8	7.0	-56%	36	45	21%
	97-07-28	H065	04/09/01	25.5	12.8	-50%	44	53	18%
		H165	07/09/01	6.8	3.8	-44%	44	54	18%

[1] see Olesiuk (1999) for locations of haulouts.

APPENDIX II: Recording Sessions of Transient Killer Whales Analysed in this Study

Table A-III: List of recording sessions from California.

Date (yy-mm-dd)	Location	Recorded by	Individuals Present[2]			No. of Calls Total	 Used[1]
83-01-16	Soberanes Pt.	R.Bolt,C.Malme L.Beranek, R.Newman, R.Mlawski	N/A			10	2
84-11-18	Monterey Bay	G. Silber	CA095			6	1
87-10-08	Monterey Bay	N. Black	N/A			166	111
92-05-02[3]	Monterey Bay	D. Goley	T132,	T134,	T135 + at least 14 others	543	368
99-05-00	Monterey Bay	R. Ternullo	N/A			367	192

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[1] Number of calls with a quality rating of three or higher (see Methods of Chapters II and Chapter V for details).

[2] Identification names according to Black *et al.* (1997) and Ford & Ellis (1999).

[3] See Goley & Straley (1994) for details.

Table A-IV: List of recording sessions from British Columbia.

Date	Location	Recorded by	Individuals Present[2]	No. of Calls	
(yy-mm-dd)				Total	Used[1]
70-05-05	Pedder Bay	P. Spong	T001, T002, + possibly others	237	179
76-03-10	Budd Inlet	G. Ellis	T013, T014, T046, T047	80	2
79-10-15	Neck Pt.	G. Ellis	T001, T002, T002B	4	0
80-08-09	Pt. Hardy	J. Ford	T034, T035, T036, T037, T038, T045	7	0
80-08-12	Deserter I.	J. Ford	T034, T035, T036, T037, T038	261	103
85-01-01	Queen Charlotte Strait	A. Morton	T010, T010A, T010B T011, T011A,	12	6
85-04-02	Blackfish Sound	J. Borrowman, G. Ellis	T007, T007A, T007B, T012, T012A, T012B, T029	55	4
85-09-25	Hammond Bay	M. Bigg	T007B, T010, T010A, T010B, T011, T011A, T018, T019, T019A, T067	26	14
85-10-04	Millar Group	J. Ford	T020, T021, T021A, T022	5	2
85-10-21	Tribune Channel	A. Morton	T007, T020, T021, T022 + possibly others	63	6
86-02-27	Tribune Channel	A. Morton	T010, T010A, T010B, T011, T011A, T018, T019, T019A	60	34
87-09-01	Albert Head	R. Baird	T010, T010A, T011, T011A, T031, T032, T033, T044, T109	1	0
87-09-27	Victoria	R. Baird	T010, T010A, T010B, T044	75	4
88-08-20	Blackney Pass	H. Symonds	N/A	92	18

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Table A-IV cont.

Date	Location	Recorded by	Individuals Present[2]	No. of Calls	
(yy-mm-dd)				Total	Used[1]
88-08-21	Deserter I.	J. Ford	T002, T002B, T018, T019, T019A, T082	127	20
88-08-31	Naka Creek	J. Ford	T001, T002 + possibly others	1	1
88-09-11	Numas I.	R. Hobbs	T020, T021, T022, T108, T109	24	1
89-12-28	Echo Bay	A. Morton	T007, T007A, T007B, T007C	87	8
91-07-17	Nob Rock	B. Ford	T070, T118, T121	4	0
91-08-10	Collision Bay	L. Nichol	T012, T012A, T012B, T070, T108, T118, T121	1	0
93-06-08	Gordon I.	Bluewater Adventures	T007, T007A, T069, T069A, T069B	16	3
94-05-12	Tofino	R. Palm	T020, T021, T022, T023, T023C, T023D, T024, T025	105	34
94-09-12	Lennard I.	R. Palm	T002, T002B, T002C, T010, T010B, T011, T011A, T013, T020, T022, T023, T041, T041A, T044, T059, T060, T109, T109A	102	22
95-05-15	Laskeek Bay	R. Burke	T040, T070, T071, T071A, T118, (T121)[3], T086, T086A	176	64
95-08-04	Clayoquot Sound	R. Palm	T012, T012A, T012C	4	2
95-08-13	Tofino	K. Davidson	T031	12	0
95-08-14	Tofino	R. Palm	T012, T012A, T012C	24	11
95-08-24	Goletas Channel	G. Ellis	T002B, T018, T019, T019B, T020, T021, T022, T028, T028A, T059, T060, (T060A)[3], T069, T069A, T069C, T139, T140, T141, T146	104	41

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Table A-IV cont.

Date	Location	Recorded by	Individuals Present[2]	No. of Calls	
(yy-mm-dd)				Total	Used[1]
96-08-25	Numas I.	F. Thomsen	T013, T014	39	20
96-09-03	Clayoquot Sound	R. Palm, K. Davidson	T012, T012A, T012C	26	12
96-10-06	Cormorant Bay	J. Borrowman	T002, T002C, T024, T025, T059, T059A, T060	3	0
97-01-31	Nanaimo	G. Ellis	T013, T014, T090, T124, T124A, T124A1, T124B, T124C, T124D	49	31
99-01-04	Hardy Bay	J. Borrowman	T011, T011A, T012, T012A	232	97
99-08-16	Blackfish Sound	V. Deecke, G. Ellis	T018, T019, T019B, T020, T021, T022	155	6
00-01-19	Nanaimo	G. Ellis	T014, T101, T101A, T101B, T102, T124, T124B, T124C, T124D, T124E	24	0
01-01-08	Blackfish Sound	P. Spong	N/A	223	25
37407	off Holford I.	V. Deecke	T002, T002C, T020, T021	5	0
01-08-17	Goletas Channel	V. Deecke	T055, T055A, T055B, T069, T069A, T069C, T069D	89	1
02-08-22	Gordon Channel	V. Deecke	T018, T019, T019B, T019C, T142, T143	416	107
02-08-23	Bates Pass	V. Deecke	T002B, T010, T010B, T010C, T018, T019, T019B, T019C, T059, T059A, T060, T060C, T109, T109A, T109B, T109C, T142, T143	53	0
02-08-27	Port McNeill	R. Hicker, B. Mackay	T014, T069, T069A, T069C, + one other	56	26

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[1] Number of calls with a quality rating of three or higher (see Methods of Chapters II and Chapter V for details).

[2] Identification names according to Ford & Ellis (1999).

[3] Identification names in brackets refer to animals that could not be identified unequivocally from the photographs.

Table A-V: List of recording sessions from Southeast Alaska.

Date	Location	Recorded by	Individuals Present[2]	No. of Calls	
(yy-mm-dd)				Total	Used[1]
83-08-13	SE Alaska,	D. McSweeney	T101 + possibly others	73	25
83-08-31	Stephens Pass	D. McSweeney	T063, T064	27	11
86-06-27	Five Fingers	Bluewater	T071, T086, T124, T124A	12	2
91-06-15	Glacier Bay	C. Gabriele	T087, T088, + 4 others	31	5
91-07-19	Frederick Sound	J. Jacobsen	T023, T023C, T024, T025, T063, T065, T065A	6	0
91-07-22	Frederick Sound	J. Jacobsen	T034, T036, T091, T092	21	6
91-08-12	Tracy Arm	J. Ford	T066, T072, T075, T075A, (T076)[3], T077, T078	15	0
97-06-21	Stephens Pass	V. Deecke, B. Falconer	T064, T064A	37	8
99-06-08	Glacier Bay	V. Deecke, E. Saulitis	T087, T088	8	2
99-06-11	Icy Strait	V. Deecke, E. Saulitis	T101, T101A, T101B, T102	16	0
99-06-15	Icy Strait	V. Deecke, E. Saulitis	T086, T086A, T103, T104	6	0
00-06-27	Glacier Bay	D. Matkin	T023, T023C, T023D, T024, T025, T085, T085A, T085B, T090, T090A, T124A, T124A1	2	1
47292	Glacier Bay	D. Matkin	T002, T002C, T023, T023C, T023D, T024, T025, T085, T085A, T085B, T087, T088, T090, T090A, T091, T092, T124A, T124A1	14	0
00-07-01	Icy Strait	D. Matkin	T075, T075A, T075B, T075C, T077, T077A, T077B, T078	2	0

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Table A-V cont.

Date (yy-mm-dd)	Location	Recorded by	Individuals Present[2]	No. of Calls Total	 Used[1]
00-07-07	Glacier Bay	V. Deecke, H. Yurk	T036, T036A, T036B, T063, T065, T065A, T065A1, T065B	135	6
00-07-12	Glacier Bay	V. Deecke, H. Yurk	T073, T073A, T073B, T073C, T074, T079	10	3
01-06-27	Tracy Arm	V. Deecke	T087, T088, T090, T090A, T101A, T102, T124, T124A, T124A1, T124A2, T124B, T124B1 T124C, T124D, T124E	354	174
01-06-28	Endicott Arm	V. Deecke	T090, T090A, T124, T124A, T124A1, T124A2, T124B, T124B1, T124C, T124D, T124E	121	50
01-07-10	Glacier Bay	V. Deecke, D. Matkin	T090, T090A, T124A, T124A1, T124A2	15	1
01-07-13	Glacier Bay	V. Deecke, D. Matkin	T090, T090A, T124A, T124A1, T124A2	8	0

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[1] Number of calls with a quality rating of three or higher (see Methods of Chapters II and Chapter V for details).

[2] Identification names according to Ford & Ellis (1999).

[3] Identification names in brackets refer to animals that could not be identified unequivocally from the photographs.

APPENDIX III: Spectrograms of the Call Types of West Coast Transient Killer Whales

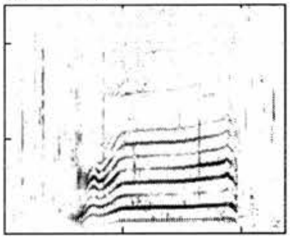
Remarks

Spectrograms were generated using custom-written sound analysis software programmed in MATLAB (The MathWorks Inc.) using a sampling rate of 44.1 kHz, an FFT size of 4096 samples, a frame length of 512 samples and an overlap of 75% between frames. A Hamming window was used for normalisation. These parameters yielded a time resolution of 2.092 ms, and a frequency resolution of 10.767 Hz. To improve visual clarity, an average noise spectrum, calculated from the spectrogram section immediately before the onset of the call was subtracted from each time bin. Call types are named with the population identifier WCT (for West Coast transient) followed by a two-digit number. Wherever call types are largely consistent with those of Ford (1984) and Ford & Morton (1991), their original numbers are retained. Recording sessions are labelled in the format yy-mm-dd. The spectrogram of the best optical quality is shown for each recording session. Recording sessions yielding only calls with quality ratings of three or lower (see methods Chapter II, Chapter V for information on quality ratings) are generally omitted. Where space permitted (call types WCT09, WCT10, WCT12, WCT14, and WCT15), several examples are shown for each recording session.

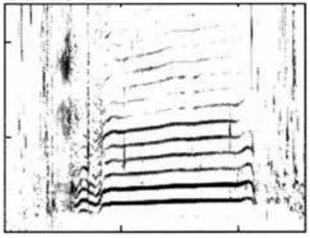
WCT01

California

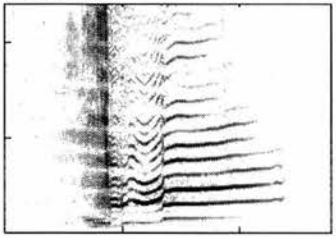
87-10-08



92-05-02

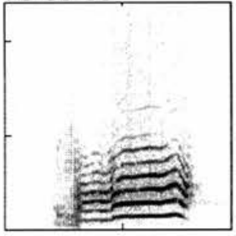


99-05-00

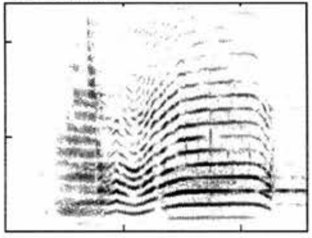


British Columbia

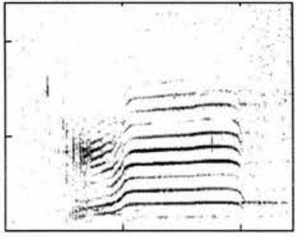
70-05-05



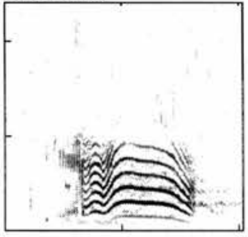
80-08-12



85-01-01



86-02-27



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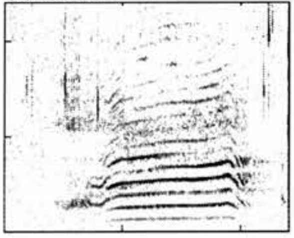
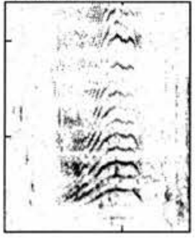
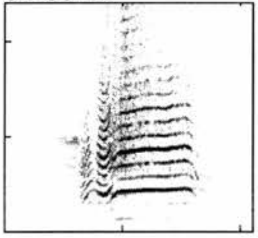


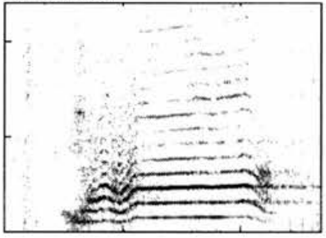
88-08-21



94-09-12



95-05-15



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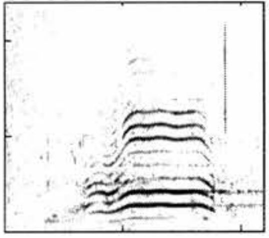
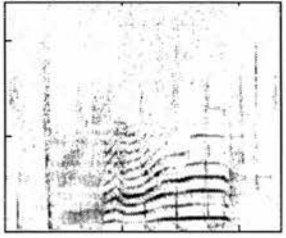
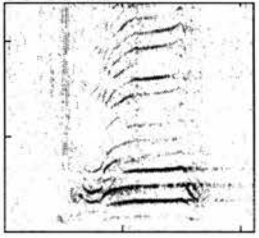


96-09-03



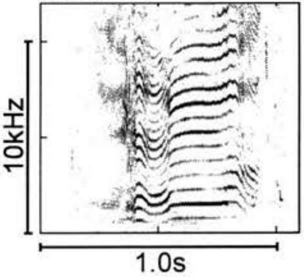
99-08-16



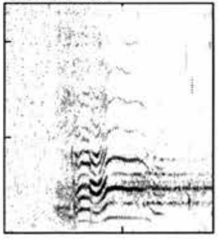
02-08-22

Southeast Alaska

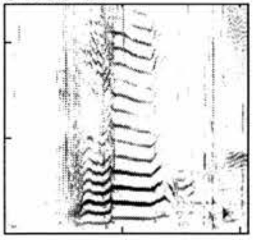
83-08-13



83-08-31



01-06-27



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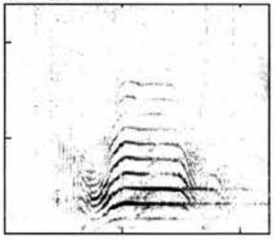
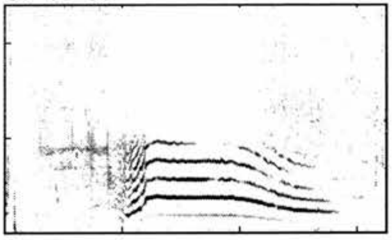


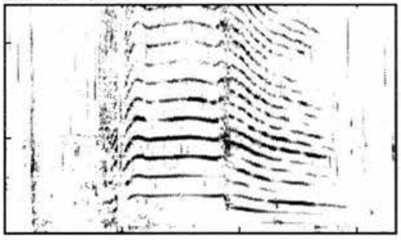
WCT02

California

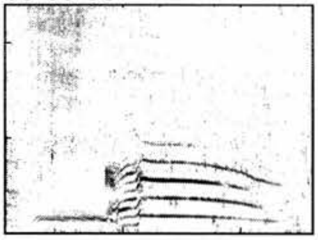
87-10-08



92-05-02

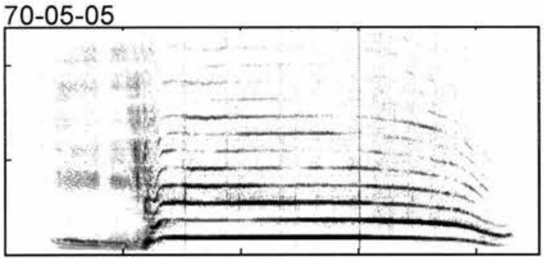


99-05-00

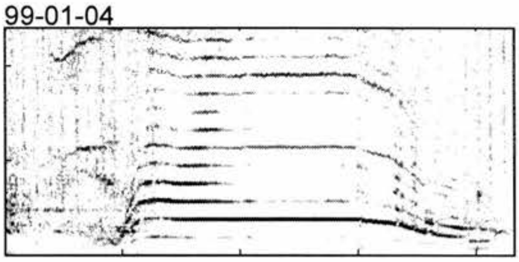


British Columbia

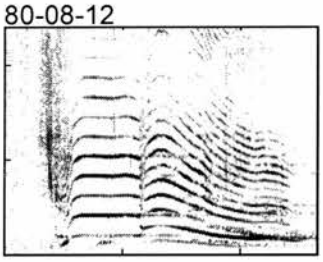
70-05-05



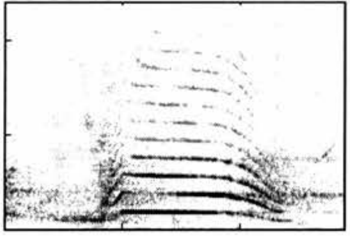
99-01-04



80-08-12



95-05-15



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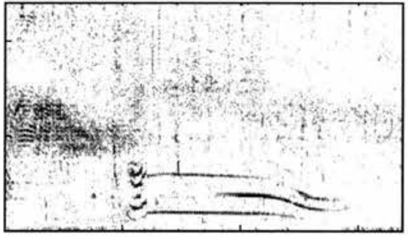
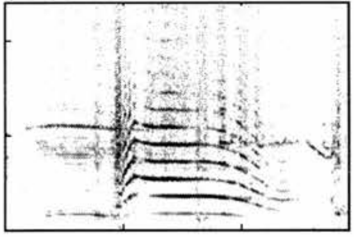
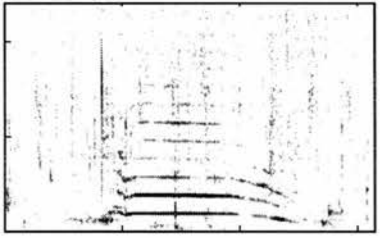


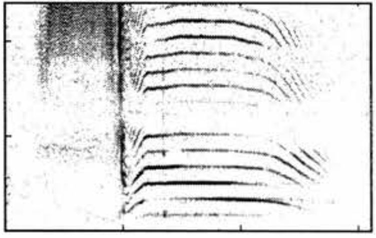
94-09-12



96-09-03

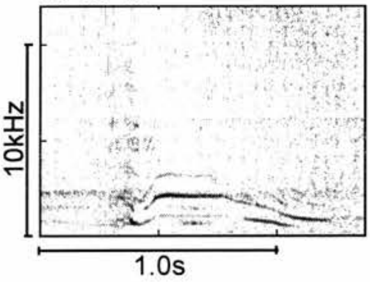


02-08-22

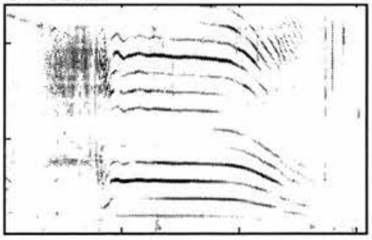


Southeast Alaska

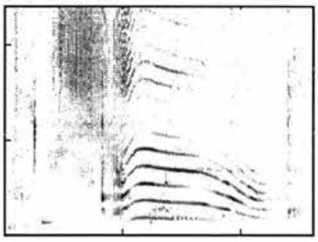
83-08-31



01-06-27



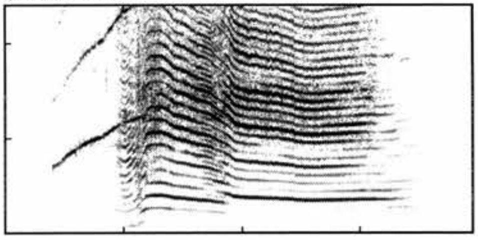
01-06-28



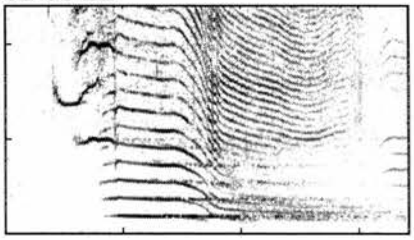
WCT03

British Columbia

97-01-31

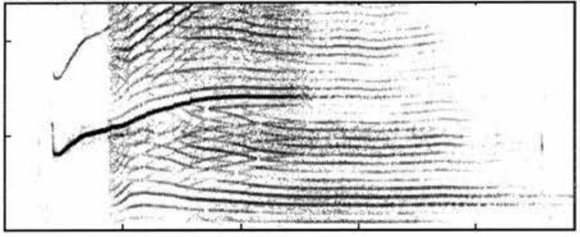


02-08-22



Southeast Alaska

01-06-27



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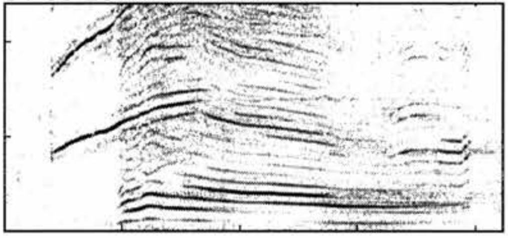
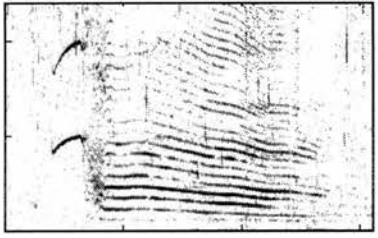


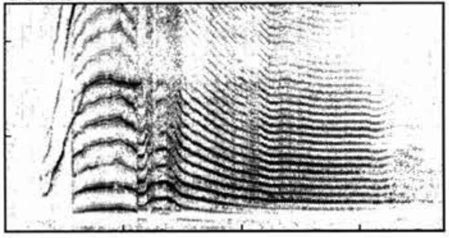
83-08-13



WCT04

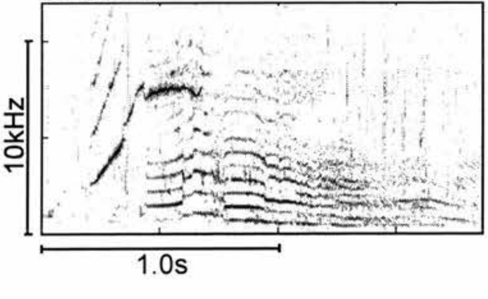
British Columbia

80-08-12

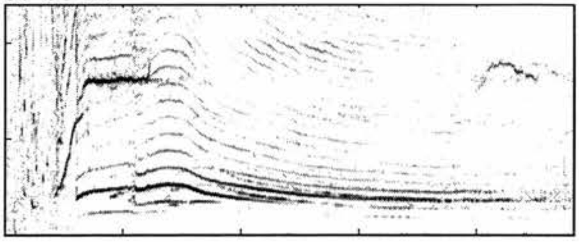


Southeast Alaska

91-07-22



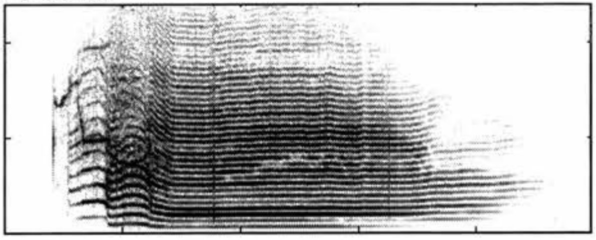
97-06-21



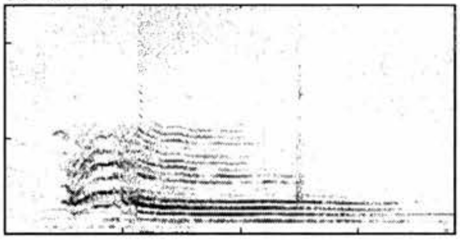
WCT07

British Columbia

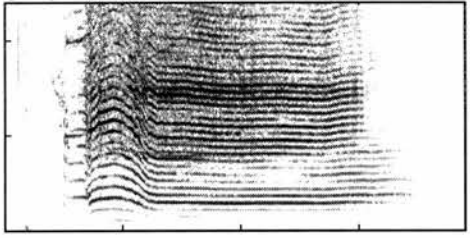
70-05-05



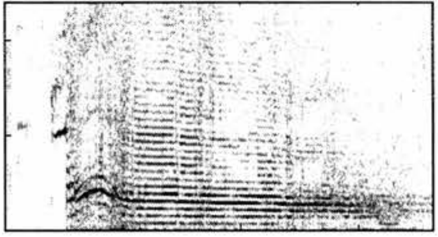
89-12-28



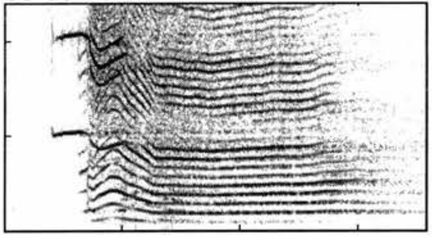
97-01-31



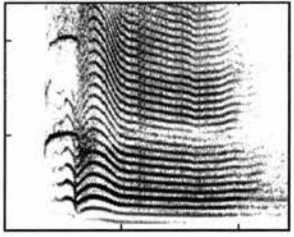
99-01-04



96-08-25



02-08-22



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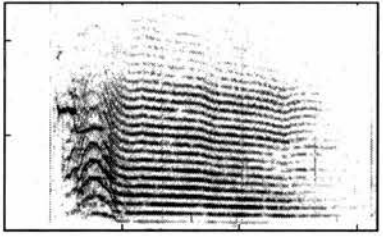
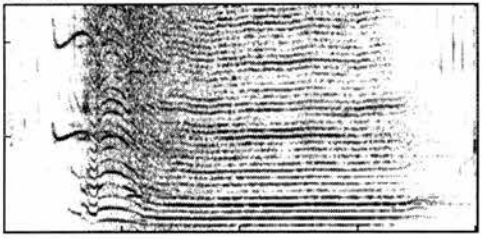
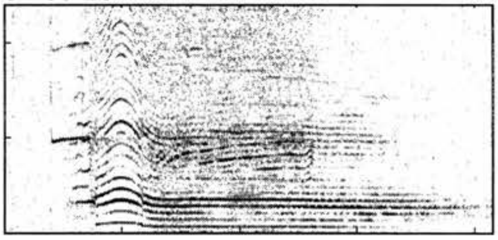


Southeast Alaska

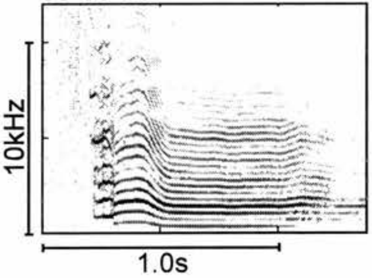
01-06-27



01-06-28



83-08-13

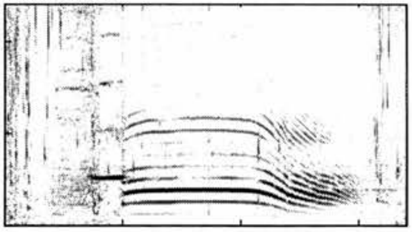


WCT08

California

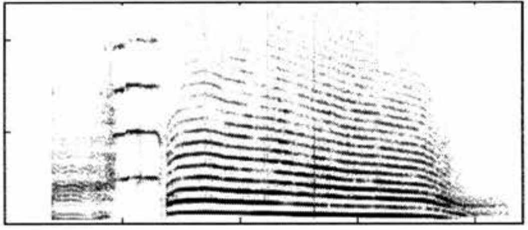
87-10-08

92-05-02

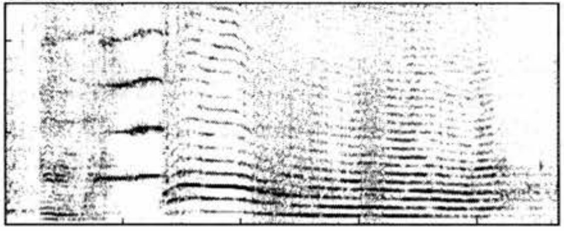


British Columbia

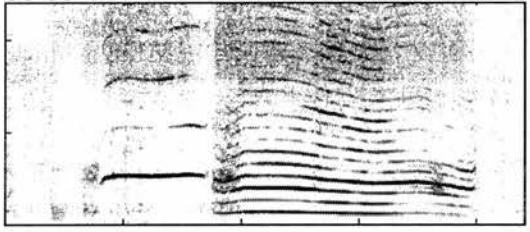
70-05-05



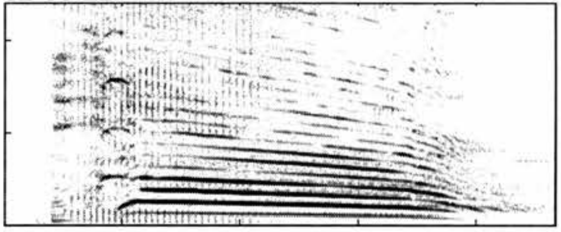
99-01-04



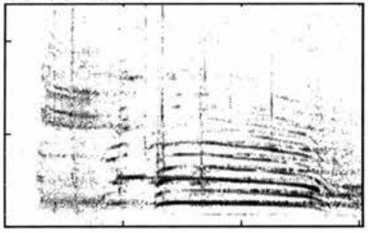
95-08-14



02-08-22

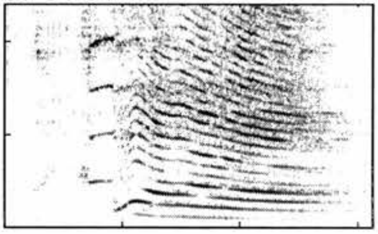


80-08-12



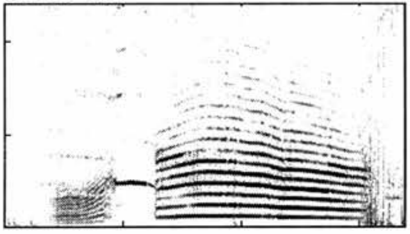
96-08-25

97-01-31



Southeast Alaska

83-08-13



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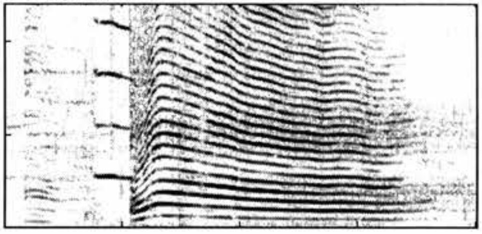
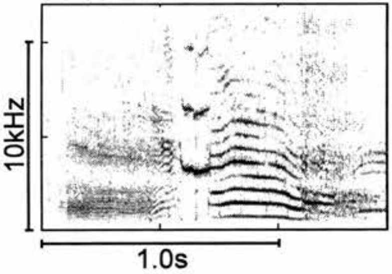


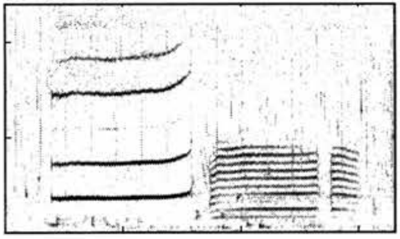
91-07-22



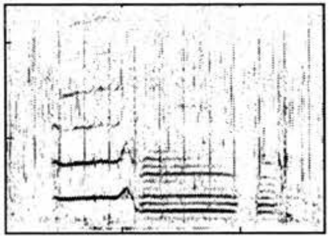
WCT09

California

87-10-08



87-10-08



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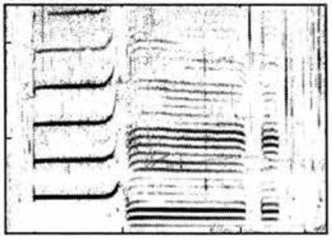

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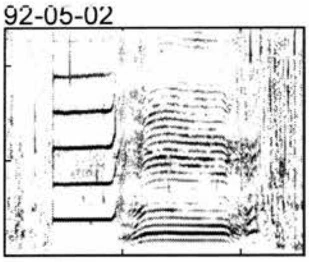
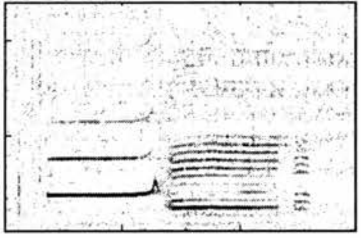


99-05-00



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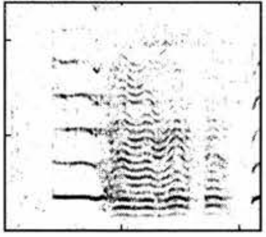
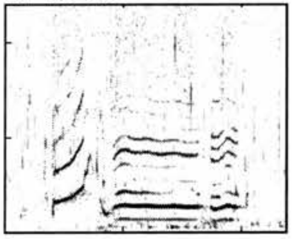


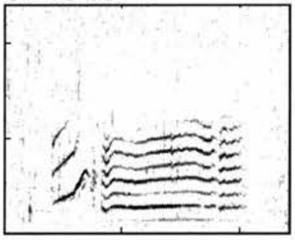
WCT10

California

87-10-08



87-10-08



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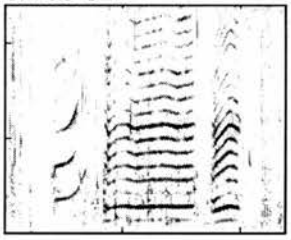

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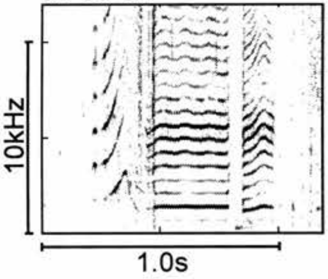
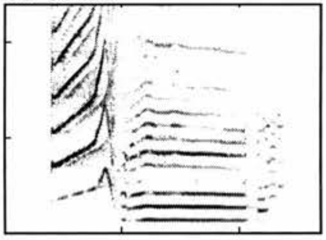


99-05-00



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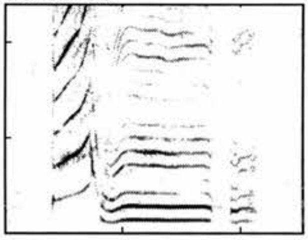
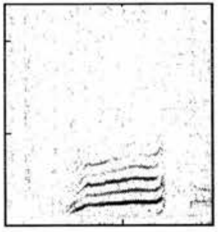


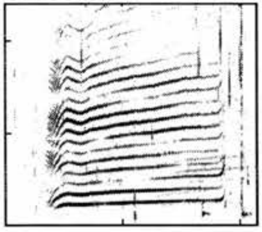
WCT11

California

87-10-08

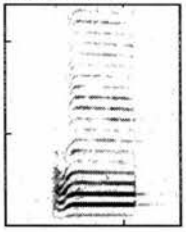


92-05-02



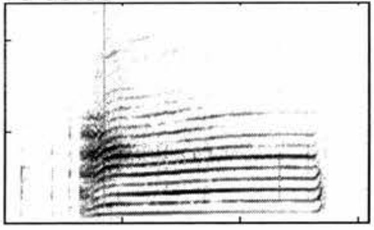
92-05-02

99-05-00

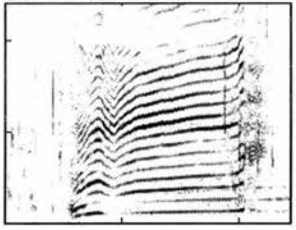


British Columbia

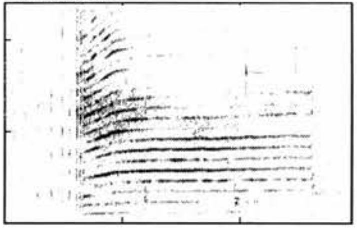
70-05-05



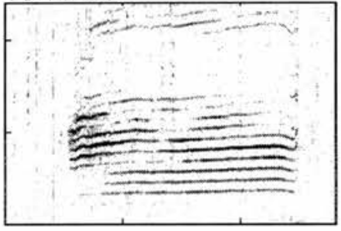
80-08-12



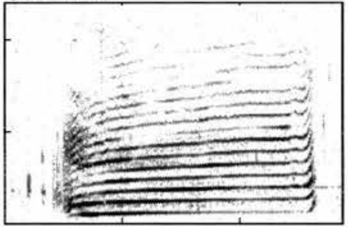
85-09-25



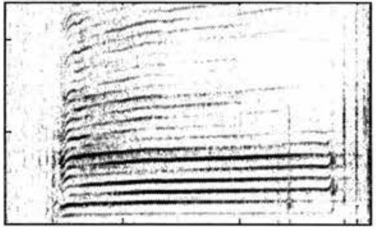
85-10-21



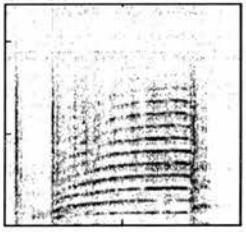
86-02-27



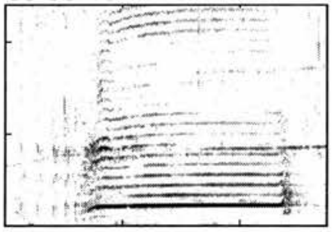
95-08-24



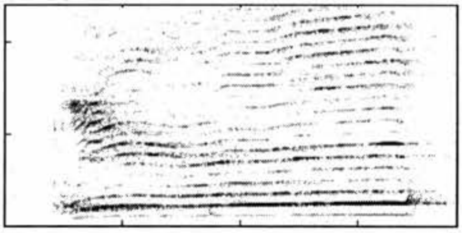
94-05-12



95-05-15



02-08-22



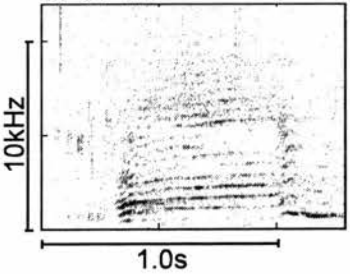
Southeast Alaska

83-08-13

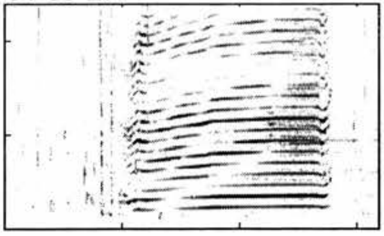
83-08-31

91-06-15

00-07-12



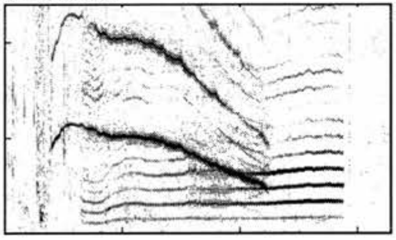
01-06-27



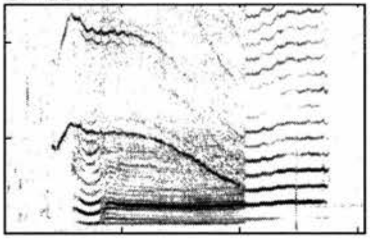
WCT12

California

87-08-10



87-08-10



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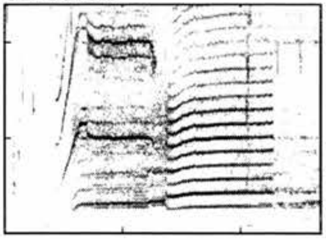

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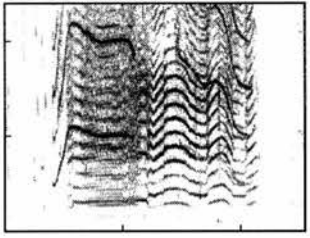
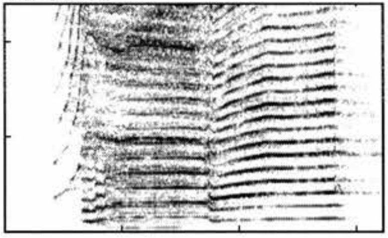
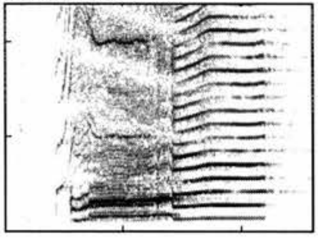


99-05-00



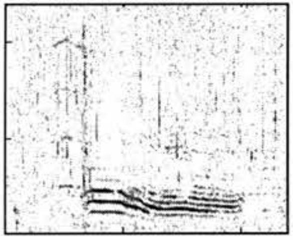
99-05-00



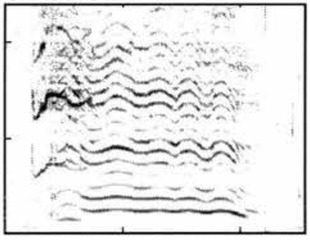
WCT13

California

87-10-08



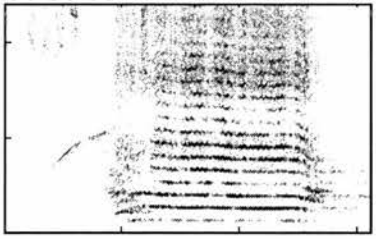
92-05-02



British Columbia

89-12-28

01-01-08



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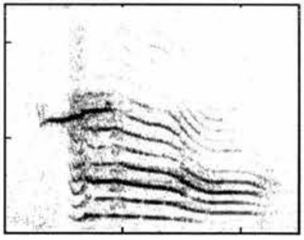
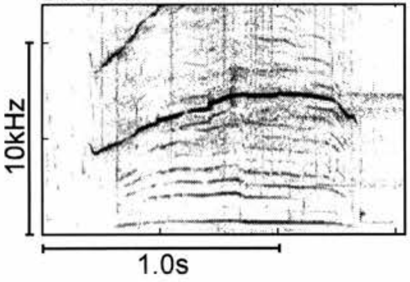


Southeast Alaska

01-06-27



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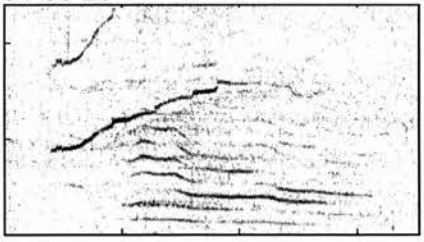
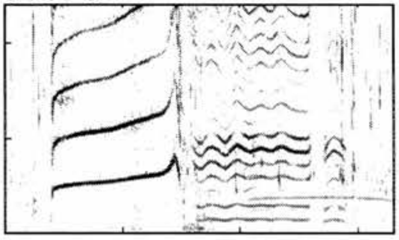


WCT14

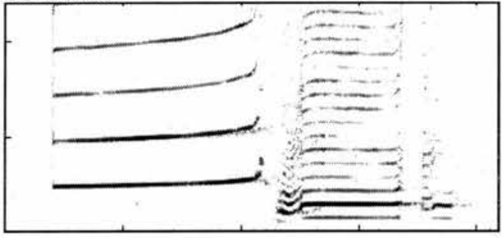
California

92-05-02

92-05-02



99-05-00



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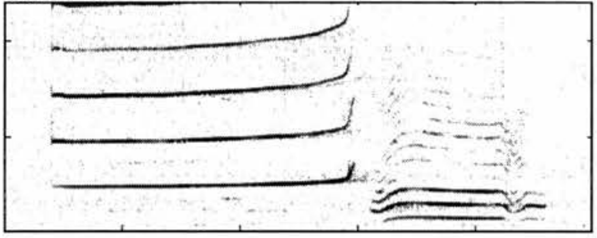
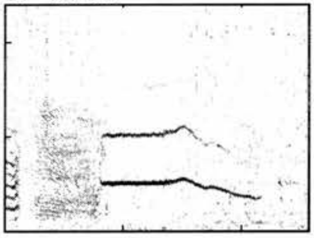


WCT15

California

87-10-08



87-10-08

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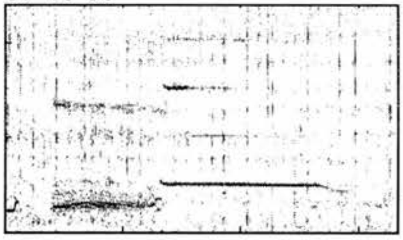

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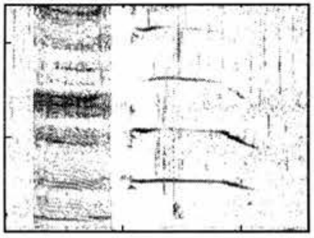

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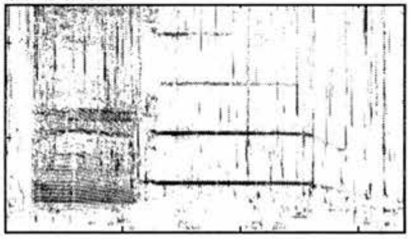

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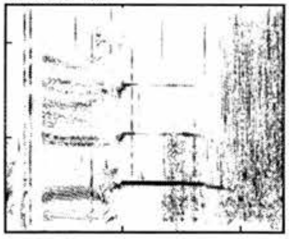

British Columbia

80-08-12