Correlates of variability in killer whale stereotyped call repertoires.

Foote, Andrew David

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Correlates of variability in killer whale stereotyped call repertoires.

by

Andrew David Foote

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Abstract

Killer whales vocalisations include repertoires of stereotyped call types (Ford 1984). There is strong evidence that these vocalisations are learnt (Hoelzel and Osborne 1986; Bain 1989; Deecke et al. 2000; Yurk et al. 2002). Call types can be group specific or shared amongst a number of groups, depending upon the social structure of the population or the call type (Ford 1991; Deecke 2003). It is thought that these call types function in the group cohesion and coordination (Hoelzel and Osborne 1986; Ford 1989, 1991; Miller 2000, 2002). Some call types contain two overlapping, independently modulated, components each having different transmission properties (Miller 2002), these call types have a higher estimated active space than single-component call types (Miller 2006).

This thesis investigates the evolution of these call type repertoires, focusing on call type usage and structure of the Southern Resident population over a period of 27 years, but including comparisons with other populations. I present evidence of hetero-specific mimicry and further evidence for vocal production and usage learning in killer whales.

I compared the relative frequency of use of call types between two time periods (1977-81 & 2001-2003) and between contexts, such as direction changes with directional travel and multi-pod aggregations with single pods. I found a strong correlation of relative call type usage for each pod between the two time periods and each pod was easily acoustically distinguishable from the other two pods in both periods. The implications of these results for a role of call type repertoires in kin recognition are discussed.

The least cohesive pod produced a significantly higher proportion of two-component call types than the other two more cohesive pods. Lone whales separated from their pod also used a rare subset of two-component call types rather than their pod's main call types. In recordings of multi-pod aggregations I recorded a high proportion of the same subset of two-component call types not commonly produced by any of the three pods individually, these call types were used in significantly higher proportions when all three pods were converging or socialising rather than travelling. These contextual correlates suggest that call types are selectively used and shared between groups based on their transmission properties.

Each of the Southern Resident pods, J, K and L, were found to increase the duration of their primary call type 10-15% in the presence of vessel noise in recordings made between 2001 & 2003. This response was not detected in recording from two earlier time periods, (1977-1981 or 1989-1992). This change in behaviour correlated with an increase over the past decade in vessel presence around this population and may be an anti-masking strategy.

I also compared the range and mean minimum and maximum fundamental frequency of the call types within the repertoires of six North Pacific killer whale populations. There was a degree of homogeneity in the range of call type fundamental frequencies within the repertoires of populations of the same ecotype, but differences between ecotypes. Offshore call types generally had a higher pitch fundamental frequency than transient or resident call types. All three resident populations had call types in their repertoires that had a maximum fundamental frequency 3 kHz higher than found in any transient call type.

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"*When last I left you I was but the learner, Now I am the Master* (of Science)" Darth Vader

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Chapter 1 - General Introduction.

Vocalisations of many species vary across both temporal and spatial scales. These patterns of vocal variation can be due to ecological factors. If these vocalisations are passed on from one individual to another by a social learning process, patterns of variation can also be determined by the timing of dispersal relative to the period of maximal learning, rate of recruitment into a population, and the mode of cultural transmission (Slater 1986, 1989; Nettle 1999; Cavalli-Sforza 2000; Wright and Wilkinson 2001).

Transmission can occur vertically between parent and offspring in a manner analogous to genetic inheritance, but also horizontally across a generation or obliquely between members of different generations that are not directly related (Lynch 1996; Cavalli-Sforza 2000).

Sources of vocal variation include the accumulation of random copying errors, which can lead to the divergence of vocal behaviour between isolated groups in a non-directional manner (Lynch 1996; Deecke et al. 2000). Inventions of new types or innovations on old types can also cause heterogeneity within and between populations (Slater 1986, 1989; Lynch 1996; Nettle 1999; Cavalli-Sforza 2000). These last two need not necessarily lead to directionless change, vocalisations may undergo functional selection e.g. the acoustic properties of an environment may favour vocalisations with particular characteristics (Wiley and Richards 1982; Slater 1986, 1989). Social selection of vocalisations can also occur and lead to vocal convergence between associates within social groupings (Boughman 1998; Wright and Wilkinson 2001; Smolker and Pepper 1997; Watwood et al. 2004). Social and functional selection may interact and signals may by be shared based upon their transmission properties (Slater 1986; 1989).

Vocalisations are easily quantifiable and have frequently been used in the study of cultural evolution in humans (Cavalli-Sforza 1981, 2000; Boyd and Richerson 1985), birds (Ince et al. 1980; Payne 1985, 1996) and cetaceans (Payne and Payne 1985; Helweg et al. 1998; Deecke et al. 2000; Rendell and Whitehead 2003). These studies have shed some light on the mode of transmission and other determinants of cultural variation, such as rate of immigration and period of maximal learning.

In this thesis I investigate the evolution of killer whale call repertoires by quantifying change over time and comparing call usage and structure between social, behavioural and ecological contexts in an attempt to determine possible mechanisms and causes of vocal variation and further our understanding of the function of killer whale call repertoires.

Social Structure

Long-term studies of killer whales *Orcinus orca*, based in the North-eastern Pacific, pioneered the use of photo-identification of individuals, using natural markings on the dorsal fin and back, to monitor travel patterns, social structure and life history (Bigg et al.1990). They found several putative, highly structured, allopatric, parapatric and sympatric communities, which have been confirmed as discrete populations by subsequent genetic analysis (Hoelzel and Dover 1991; Hoelzel et al. 1998, 2002; Barrett-Lennard 2000) and appear to reflect the structure of killer whale populations worldwide (Hoelzel et al. 2002; Waples and Clapham 2004). Behavioural observations, stomach content, fatty acid and stable isotope analysis of identified individuals have found that populations differ in their feeding specialisations, social structure, travel patterns, site fidelity and acoustic behaviour (Ford 1984; Ford et al.

1998; Osborne 1986; Morton 1990; Baird and Dill 1995; Baird 1996; Baird and Whitehead 2000; Matkin et al. 1999; Saulitis et al. 2000, 2005; Heise et al. 2003; Deecke et al. 2005; Herman et al. 2005).

Three populations, the AT1 Transient, Gulf of Alaska Transient and West Coast Transient populations, are named *transients* as early studies found a lack of seasonality in sighting frequency (Bigg et al. 1990), although later studies found that some individuals showed seasonal site fidelity (Baird and Dill 1995). The West Coast Transient population is parapatric to both the AT1 and Gulf of Alaska transient populations, which live in sympatry with one another (Barrett-Lennard 2000). Transients forage almost exclusively on marine mammals (Baird and Dill 1995; Ford et al. 1998, Ford and Ellis 1999; Matkin et al. 1999; Saulitis et al. 2000; Heise et al. 2003) although they have been observed to prey on the occasional sea bird or land mammal (Ford and Ellis 1999). Transients have a limited carrying capacity with an optimal group size of three members (Baird and Dill 1996), leading to a more fluid social structure with exchange of individuals between groups (Baird and Whitehead 2000; Saulitis et al. 2005).

A population known as *Offshores* are infrequently sighted and poorly studied in comparison to other North-eastern Pacific killer whale populations. They are found mainly more than 15 km offshore near the continental shelf (Krahn et al. 2004), but are occasionally found in nearshore waters. This population has been sighted from California to the Aleutians (Krahn et al. 2004) and are thought to be pisciverous (Ford et al. 2000; Herman et al. 2005).

Finally three populations specialise in foraging on salmonids (Ford et al. 1998; Saulitis et al. 2000). These last three populations show a high degree of seasonal site fidelity in core areas (Morton 1990), which coincides with the salmon runs (Heimlich-

Boran 1986; Nichol and Shackleton 1996) and has led to the name *residents* (Bigg et al. 1990). This period when large aggregations occur in core areas is thought to be when most mating takes place (Olesiuk et al. 1990).

Each resident population can be further split into a nested hierarchy of social groupings; population, clan, pod and intra-pod groups, which are matrifocal. Intra-pod groups are commonly and hereafter in this thesis called matrilines (Bigg et al. 1990). The term pod refers to a group of matrilines that associate for at least 50% of the time (Bigg et al. 1990). As a pod increases in size over time the constituent matrilines travel independently for longer periods of time until they can no longer be considered a single pod (Bigg et al. 1990). The longitudinal photo-id study has revealed a lack of dispersal of either sex from the natal matriline in the resident populations (Bigg et al. 1990). The Southern Resident population is commonly delineated into three pods J, K and L pods (Bigg et al. 1990), however L pod may no longer be a true pod under the 50% definition (Krahn 2004).

Using human language as an example, Cavalli-Sforza (2000) points out that genes do not influence the adoption of a learnt behavioural trait by an individual; this is in fact a function of the time and place of birth. However behavioural differences can act as a barrier for gene flow, isolating populations and causing co-evolution of genes and socially learnt behavioural traits (Cavalli-Sforza 2000). In Northeastern Pacific killer whales reproductive isolation appears to be pre-zygotic, possibly based on behavioural differences (Hoelzel et al. 1998; Barrett-Lennard 2000). The status of sympatric ecotypes of killer whales in the Northeastern Pacific as different species based on genetic, morphological and behavioural evidence are still inconclusive and the subject of much contention (Waples and Clapham 2004), as it is not possible to determine whether the current pattern of genetic isolation is permanent or ephemeral over evolutionary timescales (Waples and Clapham 2004). In this thesis I use the term ecotype when distinguishing between transient, offshore and resident killer whale types.

Sound Production, Reception and Beam Formation.

Terrestrial mammals produce vocalisations in the muscular larynx and some have argued that it is also the source of sound in odontocetes (Reidenberg and Laitmann 1988). However there is a growing body of evidence that the nasal passages are the main sound source (Cranford 2000). X rays and endoscopy have revealed that air pressure is built up below the bony nares and then during vocalisation expelled through the phonic lips, which are under muscular control, across the nares and into the upper nasal sacks where it can be recycled into the respiratory system (Dormer 1979; Cranford 2000). The left and right phonic lips can act independently; both can act in click production, only the left pair has been observed to act in whistle generation (Dormer 1979; Cranford 2000). The fatty body in the forehead then acts as an intermediary between the production site and the underwater environment by matching the impedance of seawater (Aroyan et al. 2000). The gradient of sound velocity in the melon coupled with the reflection from the skull focus sound emissions into a highly directional beam (Aroyan et al. 2000). Ultrasound (>20 kHz) is received through fatty tissues in the right and left mandibles and channelled to the corresponding lympanic bulla (Ketten 2000; Aroyan et al. 2000). Lower frequency sounds (<20 kHz) are transmitted to the inner ear through ear canal (Ketten 2000).

Vocalisations

Killer whale vocalisations have been categorised as stereotyped calls, variable calls, whistles and echolocation clicks (Schevill & Watkins 1966; Hoelzel & Osborne 1986; Ford 1989). Echolocation clicks of resident killer whales are broadband and have a bimodal frequency structure, centre frequencies between 45 and 80 kHz, with a bandwidth between 35 and 50 kHz and source levels of 200-225 db re1µPa@1m (Au et al. 2004). Clicks are used for prey detection and navigation (Schevill and Watkins 1966; Barrett-Lennard et al. 1996; Au et al. 2004) a negative correlation between group size and echolocation use suggests that the information from the signal is shared between group members (Barrett-Lennard et al. 1996). Whistles are tones with several harmonics and a dominant frequency of 8.3 kHz produced at a mean source level of 140.2 ± 4.1 db re1µPa@1m (Miller 2006). They are thought to act as close range motivational sounds and can be stereotyped or highly variable (Ford 1989; Thomsen et al. 2001, 2002). Stereotyped whistles appear to be shared by all pods within a population and can be stable for at least 13 years (Riesch et al. 2006). Variable calls are produced at a higher rate during social behaviour (Ford 1989) and at a mean source level of 146.6 ± 6.6 db re1µPa@1m (Miller 2006).

Particular attention has been paid to the stereotyped calls and these are the focus of this study. Some stereotyped calls are purely tonal but most are produced by rapid pulses that have stereotypical, abrupt shifts in the pulse repetition rate, that produce a broadband signal, the fundamental frequency being equal to the pulse repetition rate, with harmonics at intervals of multiples of the pulse repetition rate (Schevill & Watkins 1966). This makes them simple to categorise aurally or by inspection of the spectrogram into discrete call types (e.g. Ford 1984; 1989; 1991;

Hoelzel & Osborne 1986; Saulitis 1993; Deecke et al. 1999; Yurk et al. 2002; Filatova et al. 2004). Discrimination of different call types by pattern recognition has been successfully demonstrated by humans (Yurk et al. 2002), neural networks (Deecke et al. 1999; Nousek 2004) and harbour seals, which reacted significantly stronger to playbacks of transient calls than to familiar resident calls (Deecke et al. 2002). The mean source level of Northeastern Pacific resident killer whale stereotyped call types range from 137 to 157db re1µPa@1m (Miller 2000, 2006; Veirs 2004).

Some call types show biphonation: an overlapping, tonal, high frequency component that has amplitude and frequency modulations bearing no relation to those of the fundamental of the pulsed lower frequency component (Schevill & Watkins 1966; Hoelzel & Osborne 1986; Ford 1989, Miller and Bain 2000; Miller 2002; Yurk et al. 2002). The fundamental of the high frequency component is between 2 and 12 kHz with harmonics of over 100 kHz and has been shown to be highly directional (Schevill and Watkins 1966; Bain and Dahlheim 1994; Miller and Bain 2000; Miller 2002) and occurs in call types with the greater source level and estimated active space (Miller 2006). Suggested functions of stereotyped calls include group cohesion and coordination of foraging (Ford 1984, 1989, 1991; Hoelzel and Osborne 1986; Miller 2000, 2002; Miller et al. 2004).

Call type usage varies across broad behavioural categories, but no specific call has yet been exclusively associated with one type of behaviour in fish-eating Pacific resident killer whales (Bain 1986; Morton et al. 1986; Ford 1989). However a population of Icelandic killer whales use a specific distinctive low frequency call directly preceding a tail slap when herding herring *Clupea harengus* (Simon 2004). The level of arousal seems to determine to some extent which call types are used (Bain 1986), and the structure of the calls (Ford 1989) in Pacific residents. Each of the

Southern Resident pods has a dominant call type that can account for over 50% of the relative call usage (Hoelzel and Osborne 1986; Ford 1991). Calling in marine-mammal eating transients occurs predominantly during social contexts and following a kill, presumably due to the high cost of alerting their acoustically sensitive prey to their presence (Morton 1990; Deecke et al. 2005; Saulitis et al. 2005).

Call repertoires and dialects

Vocal variation in killer whales is found at several levels: geographic location (Awbrey et al. 1982; Moore et al. 1988; Deecke 2003) ecotype (Ford 1984; Morton 1990; Barrett-Lennard et al. 1996; Deecke et al. 2005), population (Ford 1984, 1991; Saulitis et al. 2005), clan (Ford 1991; Yurk et al. 2002; Filatova et al. 2004), pod (Ford 1984, 1989, 1991; Hoelzel and Osborne 1986; Strager 1996; Yurk et al. 2002; Filatova et al. 2004), matriline (Deecke et al. 1999; Miller and Bain 2000; Nousek 2004) and individual (Hoelzel and Osborne 1986; Nousek 2004; Saulitis et al. 2005). Pods of resident killer whales in the North Pacific have a repertoire of 7 or more stereotyped call types (Ford 1984, 1989, 1991; Hoelzel and Osborne 1986; Yurk et al. 2002; Filatova et al. 2004). Recordings of individuals in captivity and in the wild using triangulation from a multiple hydrophone array indicate that all members of a pod produce the pod's complete repertoire (Ford 1989; Bain 1989; Miller 2000).

Killer whale pods that frequently associate with each other may share some call types, but not others (Ford 1984, 1991; Hoelzel and Osborne 1986; Strager 1996; Yurk et al.2002; Filatova et al. 2004). Some Pods have no call types in common despite associating for at least a few days in core areas such as Johnstone Strait (Ford 1991; Yurk et al. 2002; Filatova et al. 2004). Pods that share at least some of their call type repertoire are placed within a vocal clan (Ford 1991; Strager 1996; Yurk et al.

2002). Two sympatric clans in the Southern Alaska resident population found in Prince William Sound have different mitochondrial based haplotypes, suggesting that clans are matrilineal lineages (Yurk et al. 2002). The West Coast Transient population, which is found from California to Southern Alaska, all share some call types and therefore constitute a single clan (Ford 1987), however there is geographic variation in the frequency of use of call types and some call types are area specific (Deecke 2003). The Southern Residents belong to a single clan, J-clan, as all three pods have some call types in common, whilst other call types are unique to each pod (Hoelzel and Osborne 1986; Ford 1991).

It has been suggested that a repertoire of call types would be a more effective social identification badge than a single call type (Ford 1991) and that different call types within a repertoire may be used to coordinate the pod (Hoelzel and Osborne 1986; Miller et al. 2000). Others have argued that vocal repertoires can be a functionless epiphenomenon resulting from the vocal learning process (see Slater 1986, 1989 for reviews).

Killer whale call type repertoires can be considered true dialects, differentiated from geographic variation in vocalisations as the former term refers to vocal differences between contiguous groups of potentially interbreeding individuals not separated by geographical barriers (Conner 1982). Dialects are common in birds; in particular the songbirds (Oscines) which can have well defined geographic boundaries (Kroodsma 1996). However killer whale dialect ranges overlap and different vocal clans live in sympatry (Ford 1991; Yurk et al. 2002). A similar pattern occurs in sperm whales; social units can be allocated into acoustic clans by their coda repertoire, and social units from different clans have sympatric home ranges (Rendell and Whitehead 2003). It has been suggested that dialects may function in assortative mating (Nottebohm 1969; Jenkins 1977; Barret-Lennard 2000; Yurk 2005) and also lessen kin conflict (Treisman 1978). However as with repertoires, dialects may also be incidental by-products of the learning process and therefore functionless epiphenomena (Andrew 1962; Slater 1986, 1989). There may be a relationship between the product of cultural evolution (dialects) and the product of biological evolution (genetic structure of populations)(Marler and Tamura 1962; Mundinger 1982). Interestingly both killer whale and sperm whale social units are matri-focally philopatric (Bigg et al. 1990; Lyrholm and Gyllensten 1998; Hoelzel et al. 2002). Group specific dialects have been found in killer whales in other study areas such as Iceland, Norway and Russia (Moore et al. 1988; Strager 1995; Filatova et al. 2004) and so seem to be the norm for this species.

Dialects can arise through selection and/or mutation during the transmission process, either genetically or by social learning, from one individual to another (Lynch 1996). Evidence for production learning of vocalisations in killer whales although equivocal is strong (see Janik and Slater 1997; Yurk et al. 2002 for reviews) and seems the most parsimonious explanation for the development of call type repertoires in killer whales and consequently group specific dialects. Reports of captive adult killer whales adopting tank-mate's call repertoires suggest this ability may be open-ended (Bain 1989; Ford 1989).

A high correlation of genetic and acoustic variation (Yurk et al. 2002) suggests a primarily vertical transmission of vocal behaviour. However there is evidence of horizontal transmission of call types between individuals (Ford 1984; Bain 1989; Deecke et al. 2000). Changes in call structure over time are maintained between matrilines in the wild (Deecke et al. 2000) and association patterns between matrilines and call structural similarity are highly correlated (Miller and Bain 2000) suggesting vocal copying occurs between matrilines as well as within them (Deecke et al. 2000).

Objectives

Resident killer whales have a probable open-ended vocal learning ability and unusual life histories: natal philopatry, site fidelity, longevity, and social and genetic isolation likely based upon behavioural traits. They therefore make a highly stimulating subject for studying the evolution of their vocal behaviour. In the following chapters I examine evidence of the learning process and compare the structure and relative frequency of usage of stereotyped calls by the Southern Resident population at intervals spanning a 27 year period to investigate causes and mechanisms of the evolution of killer whale call repertoires.

Chapter 2 – Evidence for vocal mimicry, production and usage learning.

Introduction

Vocal learning can be differentiated into production learning: learning to alter the physical structure of the sounds by manipulation of the sound production organs as a result of experience with those of others (Janik and Slater 2000), and contextual learning, in which the comprehension or usage of a signal are learnt to be associated with a novel context (Janik and Slater 2000).

Many mammalian species have voluntary motor control over the usage of their vocalisations and learn the context in which to use a call (Janik and Slater 1997; Seyfarth and Cheney 2003). However production learning, although widespread in birds, is comparatively rare in mammals (Janik and Slater 1997). The few confirmed species so far come from a wide range of taxa: bats, primates, pinnipeds, and cetaceans, suggesting separate evolutionary pathways (Janik and Slater 1997).
Vocal production learning starts with a sensory learning phase in which listening and memorising of vocalisations from an adult tutor(s) takes place (Doupe and Kuhl 1999; Wilbrecht & Nottebohm 2003). This is typically followed by a sensorimotor learning phase in which the learner develops the motor skills necessary for normal adult vocal production by audition and matching its own vocalisations to a memorised template of those of the tutor (Marler 1991; Doupe and Kuhl 1999; Wilbrecht & Nottenbohm 2003). These early vocalisations are often highly irregular e.g. babble in infants (Doupe and Kuhl 1999), and subsong and plastic song in birds (Marler and Peters 1982), but gradually become more structurally stereotyped and adult-like with practice. However this sequence of ontogenetic change in vocal patterns is not in itself

evidence of vocal production learning as it may simply be due to physical maturation of the sound production organs (Janik and Slater 1997).

Additional evidence for vocal learning can come from deafening experiments, social isolation, dialects and geographic variation, however there are caveats associated with each of these (see Janik and Slater 1997; Egnor and Hauser 2004 for reviews). Unequivocal evidence can be obtained by training an animal to produce novel sounds not found in its natural repertoire by conditioning or cross fostering with another species (Janik and Slater 1997; Egnor and Hauser 2004).

Production and usage learning of vocalisations in killer whales have yet to be demonstrated unequivocally (Janik and Slater 1997; Yurk et al. 2002). The calls of calves have been reported as being highly irregular (Hoelzel and Osborne 1986; Bowles et al.1988). A study that tracked the first year of vocal development of a captive Icelandic killer whale calf found the structure of the vocalisations became more stereotyped over time (Bowles et al. 1988). At the end of the study period the calf produced the majority of its mother's repertoire (Bowles et al. 1988). However it was not possible to determine if these changes were due to learning or maturation of the vocal production organs (Bowles et al. 1988; Janik and Slater 1997).

Geographic variation and true dialects of call repertoires between sympatric social groups have also been found in killer whales (Awbrey et al. 1982; Ford 1991; Yurk et al. 2002). Parallel changes over time in call structure found between two closely associating matrilines suggests copying was taking place between them (Deecke et al. 2000). However as killer whale societies are matrilineal in structure and association patterns may be indicative of kinship (Bigg et al. 1990) it has been argued that these repertoire differences could be due to genetic factors (Janik and Slater 1997).

Resident populations of North-eastern Pacific killer whales live in stable natally philopatric, matrifocal pods from which there has been no recruitment apart from birth and no dispersal has been confirmed in three decades of observation (Bigg et al. 1990: Ford et al. 2000) except in two cases, which are the focus of this chapter. L98 (Luna) was first sighted in 1999 and A73 (Springer) in 2000 and, as their natal pods were sighted during the previous years, these are assumed to be the years they were born (Ford et al. 2000). However between their first and second year they became separated from their natal pods. L98 was then re-sighted alone in July 2001 in Nootka Sound, on the west coast of Vancouver Island, BC. A73 was re-sighted alone in January 2002 in Puget Sound, WA (Krahn et al. 2004). Both whales were located away from the core range of their natal populations (Krahn et al. 2004). They were under close observation at various times during the separation period. Killer whales of other populations had been within acoustic range of each individual for short periods of time between separation and recording. At the time of recording A73 and L98 were in their 2nd and 5th years respectively. Here I assess evidence for production and usage learning from these recordings.

Method

Recordings of the Southern Resident Population were made between 1977-1992 during vessel-based follows or from a shore-based array on analogue tape recorders: Sony TC-D5 or Nachamichi 550 with Barcus-Berry pre-amp and Gould hydrophone or fixed array; approximate frequency response: 30 Hz – 18 kHz using type II cassettes, and were digitised using Sound Forge software at a sampling rate of 44.1 kHz. Recordings made between 2001-2003 were made using a static hydrophone array consisting of 8 Cetacean Research Technology C304 hydrophones (frequency range 0.10-250 kHz) at Lime Kiln Lighthouse, Haro Strait directly on to a PC at 44.1 kHz using Sound Forge software.

Visual observations were used to note behaviour categories and identity of groups present using natural markings on the dorsal fin and saddle patch and referencing these to photo-identification catalogues (Ford et al. 2000; Van Ginneken et al. 2000). I used only recordings when all of the groups present had been visually identified. This required that all the killer whales be approximately 500 m or less of the recording station. Resident killer whale calls can be detected several kilometres away by hydrophones (Miller 2000; Deecke et al. 2005). Therefore there should be no bias in the detection of call types based on transmission properties.

Recordings of L98 were made in September-October 2003 and March 2004 from a small vessel with the engine turned off. Recordings of A73 were made in July 2002 in a holding pen in a natural bay following capture and relocation. Both were recorded at a distance of less than 500 m with a variety of hydrophones and recording equipment with a flat response between 0.1 – 20 kHz.

Spectrograms were produced for all vocalizations detected in a given recording using Canary 1.2.4 software with a filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752 ms and 21.73 Hz. Vocalizations were then classified into categories of discrete call types by aural recognition and inspection of the spectrograms using the alphanumeric categories of Ford (1987) as a reference. Human observers using pattern recognition have been shown to give biologically meaningful categorization of natural signals (Janik 1999) including killer whale call types (Yurk et al. 2002). Categorization of calls from each recording session was done without reference to notes on behaviour or groups present to avoid observer bias (see Janik 1999). Although in this thesis I have retained the alphanumeric system of Ford (1987) for the Southern Resident call types, I have treated calls S2i and S2ii, and S37i and S37ii as individual call types rather than subtypes of the same call type. The level of structural similarity between call subtypes appeared to be equivalent to that between some call types e.g. S1 and S7, and there is no indication from call usage patterns that the whales themselves perceive the subtypes as variations of the same call type. Therefore it was decided to designate all calls that could be clearly distinguished from one another both aurally and by inspection of the spectrogram as separate call types. I also did not include Fords (1987) short, grunt-like call type category S5 as this was difficult to distinguish from non-stereotyped call types or other biotic sounds.

All relative call usage comparisons were done using a Chi-square test.

Results

I analysed over 200 hours from 278 recording sessions of the Southern Residents, recorded between 1977 and 2003 and classified 16,153 calls into 28 call types (appendix i). A further 2,017 calls were unclassifiable either because they were too faint to reliably distinguish or the calls were non-stereotyped.

I identified 456 calls from 289 minutes of 6 recording sessions of L98 made in March 2004, of which 369 were classified into 4 call types (figure 2.1), 87 were unclassified as above.

I also identified over 1400 bark sounds, many of these were recorded when California sea lions *Zalophus californianus* were observed and spectrograms of these barks matched those previously reported for the underwater barks of adult male California sea lions (Schusterman et al. 1967; Schusterman and Balliet 1969; figure

Figure 2.1 Spectrograms of (**ai**) 4 examples of call type S1 recorded from L98, (**aii**) call type 1 recorded from J pod, (**bi**) 3 examples of call type S19 recorded from L98, (**bii**) call type S19 recorded from L pod, (**c**) 3 examples of call type Lu1 recorded from L98, (**di**) S16 recorded from L98, (**dii**) S16 recorded from K pod, (**e**) call type S2iii recorded from L pod. (nb. smearing of some of the spectrograms of L98 calls is due the high level of reverberation in the study area). (Filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752 ms and 21.73 Hz).

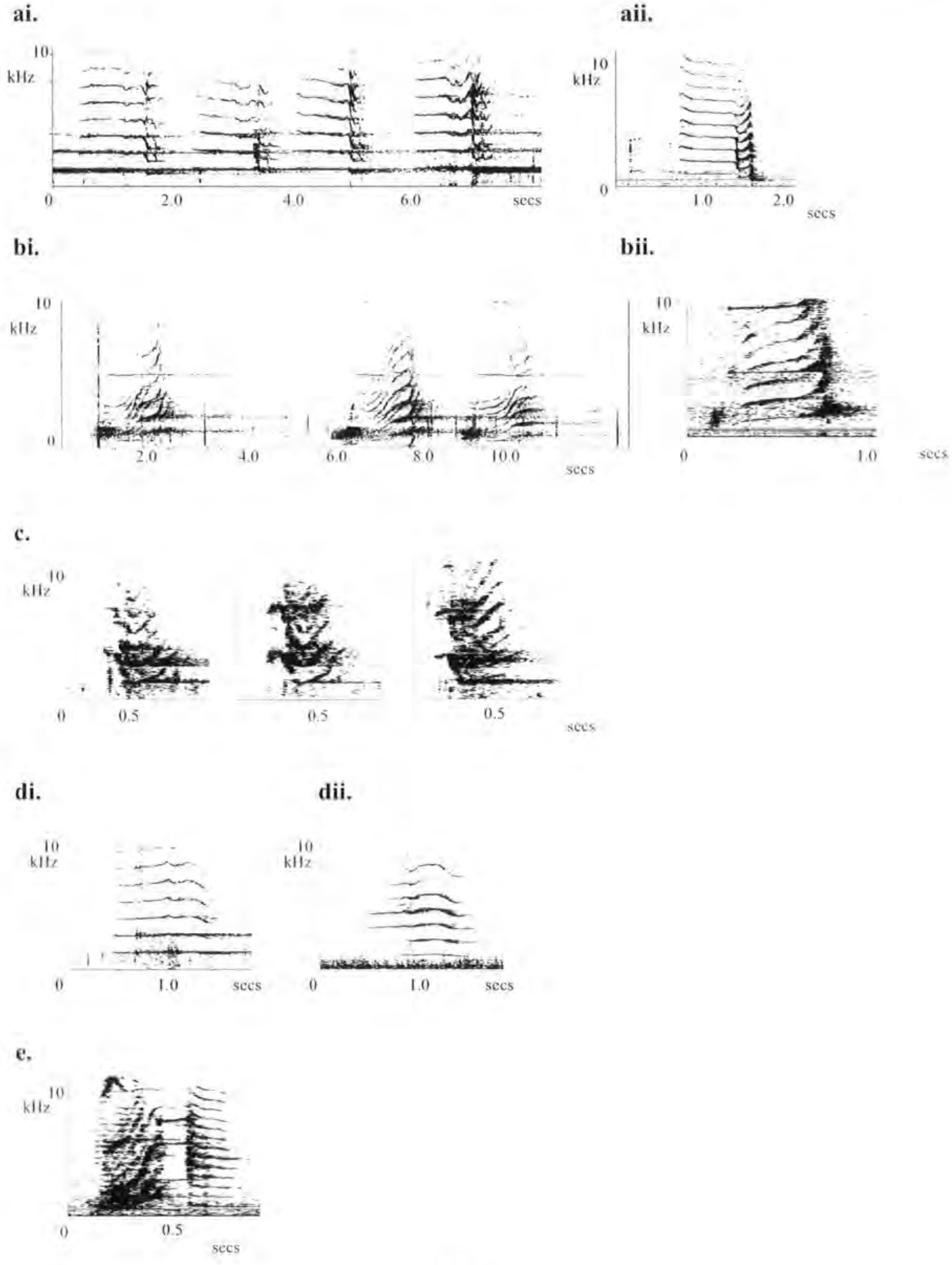


Figure 2.2a. Spectrogram of underwater barking of a California seal lion *Zalophus californianus* recorded at Tanners Bank, California 1961. **b.** Spectrogram of underwater barking recorded in Nootka Sound 2004 when L98 and California seal lions observed in the study area. **c.** Spectrogram of the underwater barking recorded in Nootka Sound 2004 when only L98 and no sea lions were observed in the study area. (Filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752 ms and 21.73 Hz).

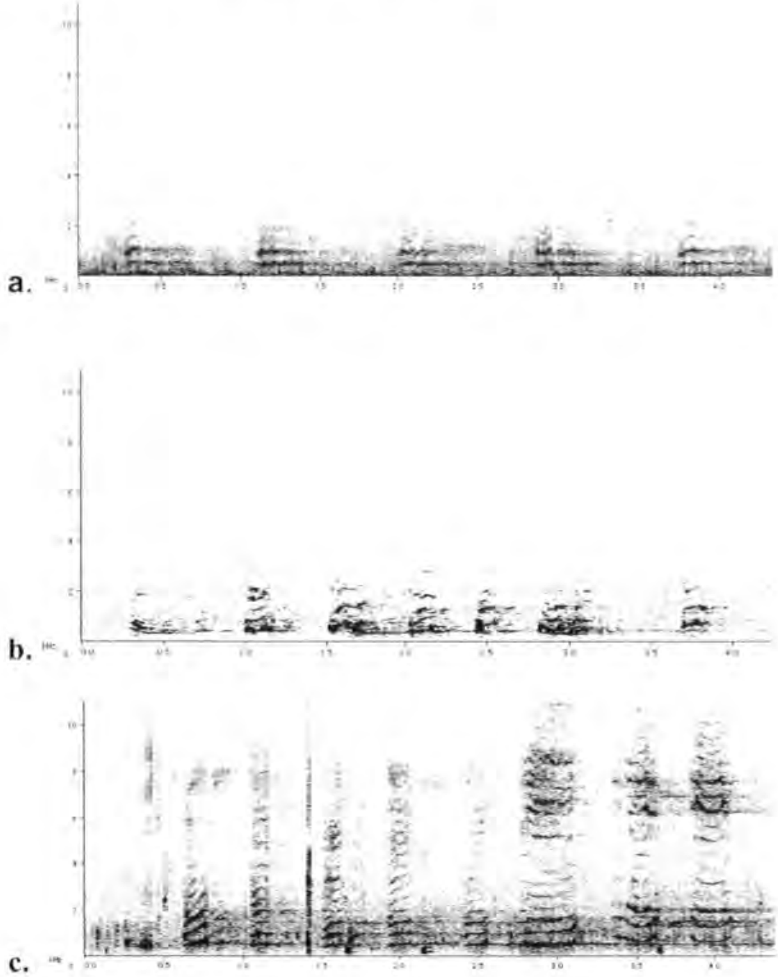
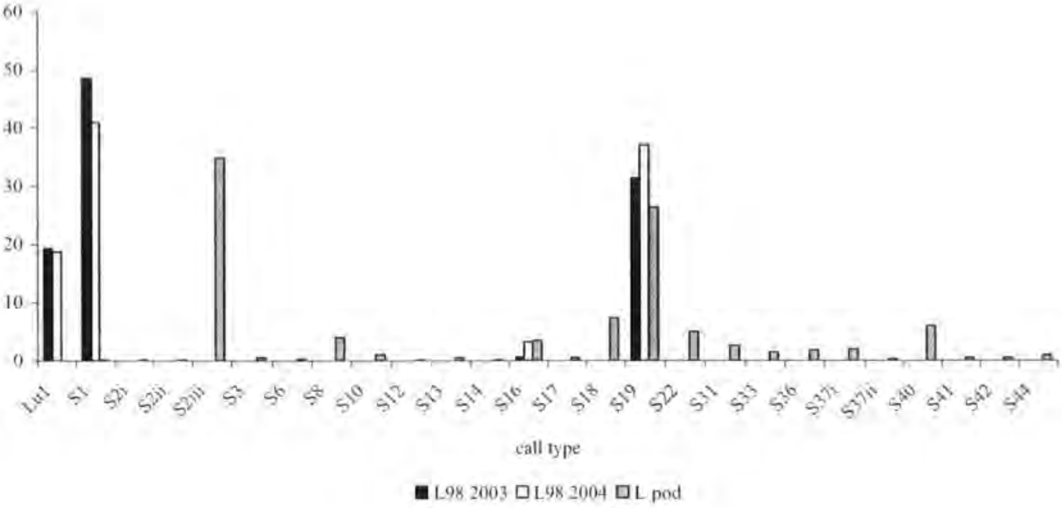


Figure 2.3 Proportional usage of call types by L pod and L98.

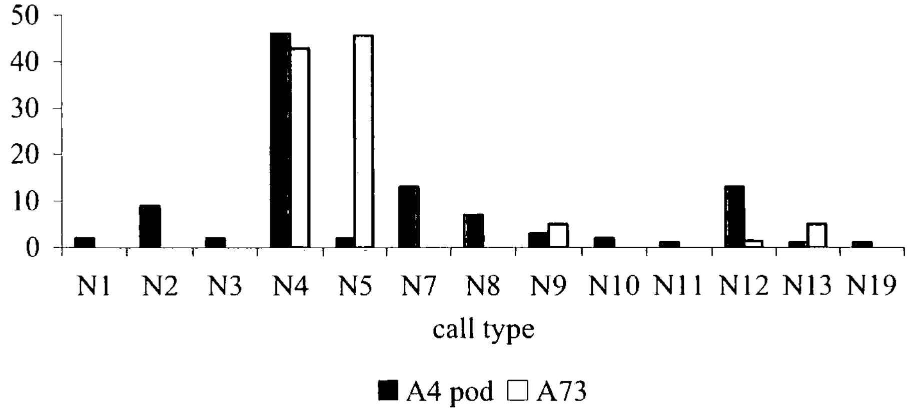


2.2). However some were recorded when only L98 and no sea lion was observed in the area, 39 of these had harmonics ranging over 10 kHz. Underwater sea lion barks typically have visible harmonics up to 4 kHz (Schusterman et al. 1967, Shusterman and Balliet 1969; figure 2.2a). Of these 39, 16 barks were recorded when only L98 and no sea lion was observed in the area, and a further 8 of those 16 barks were immediately followed regular killer whale calls or echolocation.

Excluding the bark calls, L98 still had a significantly different relative frequency of use of call types than his natal pod (L) ($\chi^2_{25} = 1901.6$, $p < 0.001$; figure 2.3). Killer whale calls are not independent events, as a call type is more likely to be repeated than followed by a different call type (Ford 1989). However recordings made six months previously indicate that there had been no change in L98's repertoire, ($\chi^2_3 = 6.52$, $p = 0.089$; figure 2.3). Thus the resultant high chi-square from the L98 and L pod comparison is not due recording L98 during a repetitive vocal bout uncharacteristic of his normal vocal output.

I analysed 106 minutes of recordings from 4 recording sessions of A73 and identified 344 calls of which 338 were classified into 5 call types, 6 were unclassified as above. I recorded 5 call types from A73: N4, N5, N9, N12, N13 (figure 2.5). All were call types commonly used by A73's natal pod (A4 pod) (Ford 1984). A4 pod's repertoire contains an additional 8 call types not recorded from A73 (Ford 1984). As I did not have precise percentage usage figures for A4 pod I could not compare the two repertoires statistically. However the use of the N5 call was clearly disproportionate when compared with that found by Ford (1984) for A4 pod (figure 2.4).

Figure 2.4 Proportional usage of call types by A73 compared with A4 pod from Ford (1984).



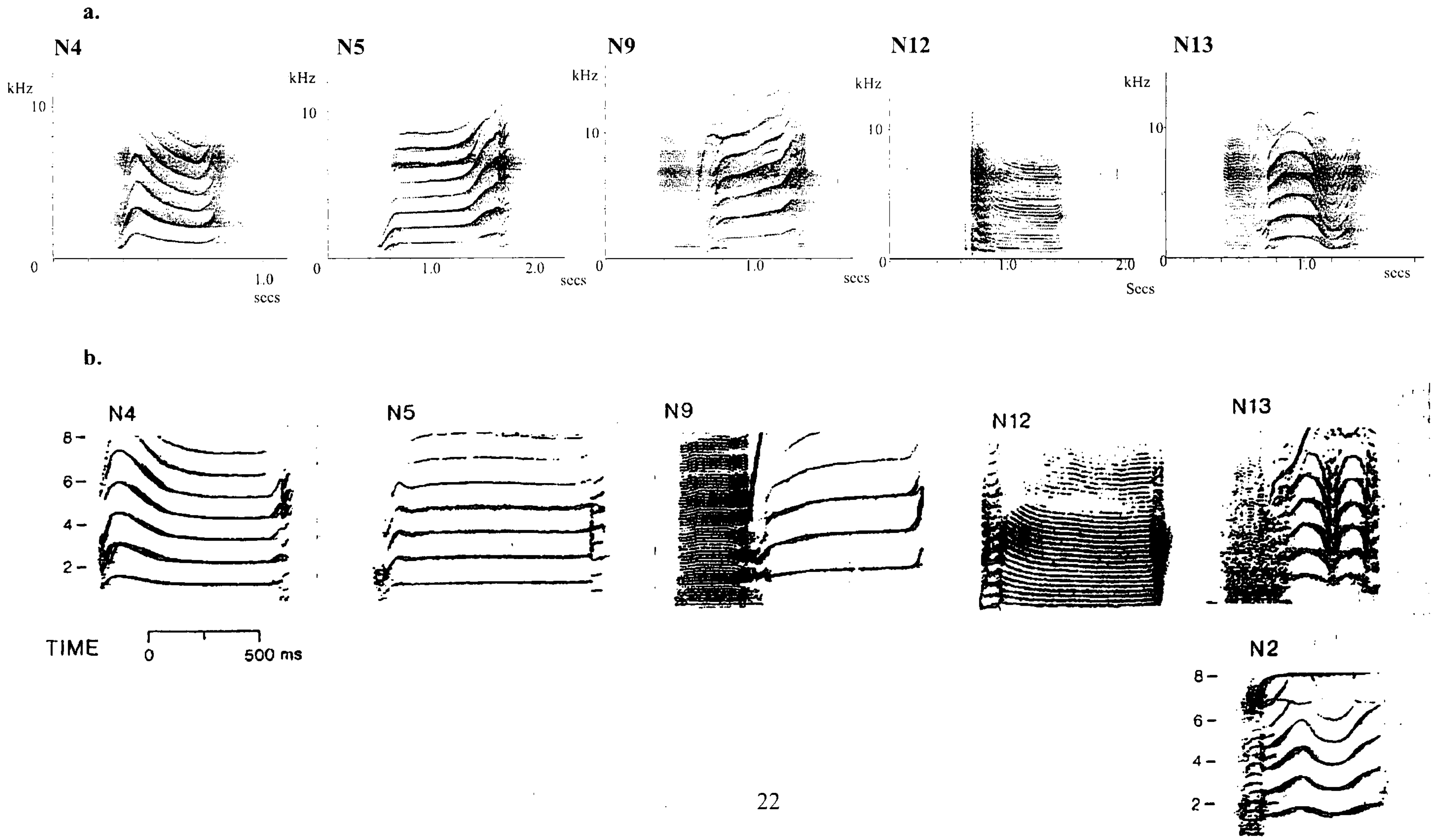
Discussion

Although I could not localise the sound source of the barks apparently made by L98, their structure and the context of the recording suggest that they were produced by L98 rather than an unseen sea lion. The high amplitude of these barks indicated the sound source was close to the hydrophone and the observation period was far longer than the maximum dive duration of a California sea lion, which is less than 10 minutes (Feldkamp et al. 1989). Therefore any sea lion would have been at the surface for at least a part of the recording and easily observable. Additionally the harmonics ranged to over 10 kHz, the frequency range of the pulsed low frequency component (LFC) of a killer whale call (Hoelzel and Osborne 1986; Ford 1987; Bain and Dahlheim 1994) and over 6 kHz above the frequency that harmonics are typically visible in spectrograms of adult male California sea lion underwater barks, in which most of the energy is found below 3500 Hz but occasionally extends to 8 kHz (Schusterman et al. 1967; Schusterman and Balliet 1969). Female California sea lions and their pups produce higher pitch barks and are very similar in character to those recorded apparently from L98 (R Schusterman personal communication), however surveys of British Columbia, including the area where these recordings were made, have found only adult and sub-adult male California sea lions (Bigg 1985). Females and pups remain south of central California throughout the year (Bigg 1985).

It is typical for killer whale calls to show harmonic loading to 10KHz or more (Hoelzel and Osborne 1986; Ford 1991; Miller and Bain 2000), but a bark-type of call had not been previously recorded for killer whales. In particular, it is shorter and has greater emphasis on lower frequencies than calls seen in documented killer whale repertoires. Taken together these data strongly imply an instance of mimicry.

The fundamental frequency of California sea lion underwater barks is a by-product of pulse rate (Schusterman et al. 1967; Schusterman and Balliet 1969) in the same way as killer whale calls (Schevill and Watkins 1966). The difference in harmonic spectral content between the barks produced by L98 and the adult sea lions may be due to the differences in the size of the resonance chambers in the vocal production organs.

Figure 2.6a. Spectrograms of call types recorded from A73 (Filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752 ms and 21.73 Hz). **b.** The same call types recorded from A clan reproduced with permission from Ford (1989). Call types N5 and N13 produced by A73 had differences in the terminal notes compared to the examples reproduced with permission from Ford (1989).



Under natural circumstances most species that learn their vocalisations have a pre-disposition to learn only conspecifics sounds (Marler 1991; Doupe and Kuhl 1999). However cross fostering and conditioning experiments have resulted in the adoption of heterospecific vocalisations in some species, e.g. song sparrows *Melospiza melodia* have learnt the song of swamp sparrows *Melospiza georgiana*, although they still showed a preference to learn conspecific song (Marler 1991). Poole et al. (2005) found two cases of vocal mimicry in African elephants *Loxidonta africana*, an orphaned adolescent imitated the sounds of trucks from a nearby road, a captive male that was housed with two female Asian elephants *Elephas maximus* produced the chirp sounds typically made by Asian but not African elephants. Social interaction has been found to reinforce vocal learning and mimicry in numerous bird species (Baptista and Gaunt 1997) and bottlenose dolphins *Tursiops truncatus* (Reiss and McCowan 1993). Additionally vocal mimicry of human speech has been reported in belugas *Delphinapterus leucas* (Eaton 1979) and harbour seals *Phoca vitulina* (Ralls et al. 1985) in captivity. Interactions between L98 and adult male California sea lions have been observed (L. Larsson personal communication) and may have prompted these cases of mimicry.

Bowles et al. (1988) were unable to determine if the vocal ontogeny they observed in a captive killer whale was due to learning or maturation. However the two whales in this study were in their 2nd and 5th years at the time of recording and did not produce the normal full range of stereotyped call types found in the repertoire of their natal pods (Ford 1984). The calls they did produce were stereotyped and could aurally be matched to those recorded from their natal pods, suggesting that the sound production organs were fully matured at the time of recording and that the underdeveloped repertoires are the result of an interrupted learning process It could be argued that the impoverished social or environmental setting may be responsible for the small repertoire sizes of these whales compared to their natal pods. Hoelzel and Osborne (1986) found a young K pod whale held in captivity produced a small number of call types and different proportional call type usage to her natal pod. However most isolated captive whales recorded to date have reproduced all or most of their natal pod's repertoire and the same relative frequency of use of call types (Bain 1986; Ford 1991). The stereotyped call type repertoire of L98 was virtually unchanged in recordings made six months apart suggesting that my results were not the result of a sampling bias of recordings of a particular context that required fewer calls. However I cannot rule out that I may not have recorded the full repertoires of both whales in the time window of the recordings.

Call type Lu1, which was recorded from L98, has never been recorded from L pod or any Southern Resident pod (Hoelzel and Osborne 1986; Ford 1987). It does resemble call type 8 of the AT1 transient population (Saulitis et al. 2005), however the AT1 transients are found in Prince William Sound, Alaska (Matkin et al. 1998; Saulitis et al. 2005) and it is unlikely that L98 has had any contact with them. This call type could be a product of innovation, invention or drift, none of which would necessarily require vocal learning (Janik and Slater 1997, 2000). However I found call types recorded from the Southern Residents between 1977-1982 were re-recorded in a recognisable form in recordings from 2001-2003 and found no new call types, suggesting that invention and innovation are rare at best and drift is too slow a mechanism to account for such a radical change in call structure. The sensorimotor phase of learning in birds often includes overproduction of song types and attrition of these down to a smaller number that are retained throughout the bird's life (Marler 1991). McCowan and Reiss (1995) found a similar pattern of whistle use by captive infant bottlenose dolphins which had a 70-80% turnover of whistle types during early periods of whistle development, and a whistle type only found in infants was gradually displaced by the dominant adult shared whistle. Therefore call type Lu1 may be a case of this type of over production, perhaps due the absence of suitable repertoire models from tutors.

L98's most common call-type, (S1), accounted for just 0.14% of L pod's repertoire, but 54.97% of J pod's repertoire. Although there is inter-pod variation in proportional call type usage (Miller and Bain 2000), L98's natal matriline (L2) was present in many of the L pod recordings and it seems unlikely that I would not have detected this call type more frequently in recordings of L pod if it accounted for a high proportion of the L2 matriline's call usage. Previous studies using a different set off recordings did not record a single example of the S1 call type from L pod (Hoelzel and Osborne 1986; Ford 1991). These findings and anecdotal reports of both captive and wild whales producing call types from other dialects (Ford 1991) suggests that killer whales have sufficient exposure to the most common calls of other pods during multi-pod aggregations for sensory learning to take place. The fact that I recorded this call so few times from L pod in the wild suggests that killer whales are able to store a template of a sound in the long-term memory and reproduce this at a much later date, with little sensorimotor experience in between, as has been found in some bird species (Marler 1991). As stated above, developing learnt repertoires often requires usage learning as well as vocal production learning. For example birds often learn a large song repertoire but select a narrow range of songs based on the song repertoires of their nearest neighbours (Marler 1991). It has been suggested that sympatric pods use call type repertoires as an acoustic badge for social identification to maintain pod cohesiveness (Ford 1989, 1991) and therefore usage learning may be important in maintaining pod-distinctive call repertoires. Production of group specific call types was found to increase immediately after the birth of a calf in two Northern Resident killer whale matrilines (Weiss et al. 2006). Bowles et al. (1988) found a year old captive Icelandic calf produced most of its mother's repertoire at 1 year of age and did not learn another female tank-mate's call types, suggesting there is individual variation in the rate of repertoire development.

Some call types contain an overlapping tonal component resulting from biphonation (Hoelzel and Osborne 1986; Ford 1987; Miller and Bain 2000). Two-component call types make up 91% of L pod's call type usage (chapter 4). L98's repertoire only contained one two-component call type, (S19), which accounted for 33% of his call type usage, but the tonal component contains little frequency modulation (figure 2.3) and may be relatively simple to produce. L pod's most common call type, (S2iii), was not recorded from L98. This is a complex call type with multiple frequency modulations in both components (figure 2.3). Possibly this call type takes longer to learn due to its complexity. Similarly bottlenose dolphins increase the number of whistle contour frequency modulations during the first year of whistle development (McCowan and Reiss 1995) and adult signature whistles are more complex than those of infants (Sayigh et al. 1990).

Many species that learn their vocalisations have a sensitive period in which most learning takes place, however there is often still some scope for vocal development post-sensitive period, e.g. human infants have a higher propensity for language acquisition than adults, but new languages can still be learnt later in life (Doupe and Kuhl 1999) That L98 appears to have learnt novel sounds after his second year suggests that at least some learning can take place later in life in killer whales. There have also been anecdotal reports of adult killer whales learning their tank-mate's repertoires (Bain 1986; Ford 1991) and of mimicry by wild whales of other pod's repertoires (Ford 1991) implying that killer whales can learn novel sounds throughout their life (Bain 1986; Ford 1991). An open-ended vocal learning ability is found in a number of species from a diverse range of taxa in which signals are shared between individuals that form long-term relationships, but in which affiliations change within an individual's lifetime (e.g. bottlenose dolphins Smolker and Popper 1999; Watwood et al. 2004, greater spear-nosed bats *Phyllostomus hastatus* Boughman 1998; Australian magpies *Gymnorhina tibicen* Brown and Farabaugh 1997, and European starlings *Sturnus vulgaris* Hausberger 1997). Although the resident killer whale populations studied in this chapter have a highly stable social structure (Bigg et al. 1990) other populations have a more fluid society with exchange of individuals between social groups (Baird and Whitehead 2000). An open-ended vocal learning ability may allow new calls to be learnt and shared between groups or individuals as new affiliations are formed.

Chapter 3 - Temporal patterns of call type usage.

Introduction

Stability of vocalisations in socially learnt vocal repertoires over a period of time can be influenced by the function of the vocalisation and the rate of immigration. Contact or monitoring signals are used to inform others of the signallers location, but often have an additional function of conveying social identity and signal affiliations between individuals, this enables the distinction between a subset of conspecifics and all other conspecifics (e.g. Brown and Farabaugh 1997; Hausberger 1997; Boughman and Wilkinson 1998 Janik and Slater 1998). The temporal stability of these vocalisations is therefore often important for social identification in stable groups. Stable shared group specific learnt vocal repertoires are found in a number of group living species that have a stable social structure (e.g. Australian magpies *Gymnorhina tibicen*, American crows *Corvus brachyrhynchos*, budgerigars *Melopsittacus undulates* Brown and Farabaugh 1997; greater spear-nosed bats *Phyllostamus hastatus* Boughman 1997; European starlings *Sturnus vulgaris* Hausberger 1997).

Although stability of call structure has been shown to exist in some marine mammals, long-term stable proportional usage has yet to be demonstrated. Bottlenose dolphins *Tursiops truncatus* have an individually distinctive signature whistle that remains structurally stable for up to at least twelve years (Sayigh et al. 1990), and accounts for up to 50% of whistle production in free ranging animals (Cook et al. 2004; Watwood et al. 2005). However the recordings from Sayigh et al. (1990) were made from restrained individuals, so it is not known if the natural proportional usage of signature whistles has remained consistent over this time period. Harp seals *Pagophilus groenlandicus* have a vocal repertoire that is stable for periods of at least up to 30 years in terms of the call types used and their structure, however proportional usage of call types varied significantly between years (Serrano and Terhune 2002). Coda output of sperm whale *Physeter macrocephalus* social units has been found to be temporally stable for up to at least six years (Rendell and Whitehead 2005). However this is only approximately 1/10 of the lifespan of a sperm whale (Rendell and Whitehead 2005). The usage of themes within Humpback whale *Megaptera novaeangiliae* song changes rapidly over a single season (Payne and Payne 1985) and they can be completely replaced by new themes over a period of two years (Noad et al. 2000).

Resident killer whales live in highly stable matrifocal pods with a total lack of immigration into or dispersal from the natal pod by either sex observed in three decades of study (Bigg et al. 1990; Ford et al. 2000). Inter-pod associations can change over periods of hours (Bigg et al. 1990). Each pod has a repertoire of seven or more highly stereotyped call types (Hoelzel and Osborne 1986; Ford 1991; Yurk et al. 2002), sharing some call types with other pods while other call types are pod specific (Hoelzel and Osborne 1986; Ford 1991; Yurk et al. 2002). The proportional usage or inter-pod sharing of these call types does not appear to be strongly linked to inter-pod association (Ford 1991), but there is some broad variation in call usage between behavioural contexts (Hoelzel and Osborne 1986; Ford 1989; chapter 4). Killer whales appear to learn both the production and usage of these call types (chapter 2). Ford (1991) previously found that killer whale stereotyped call types remained in a pod's repertoire for periods of up to 28 years. In this chapter I look at the proportional call usage of the three Southern Resident pods over a period of 27 years.

Method

See chapter 2 for acoustic recording and call type analysis methodology.

Recordings were compared between two time periods 1977-1981 and 2001-2003.

I did not use recordings in which groups changed direction as we only had recordings of group direction changes for the second period and this may have affected the proportional call usage for this time period (see chapter 4). The relative usage of each pod's two most common call types was also compared between each time period. The production of a particular call type is not an independent event as a call type is more likely than expected by chance to be followed by the same call type (Ford 1989; Miller et al. 2004), therefore I used a Mann-Whitney *U* test to compare the mean relative usage of that call type per recording session recording between the two time periods. I compared only the two most common call types to ensure an adequate sample size from both time periods.

Results

See chapter 2 for the number of recording sessions and call types categorised.

Consistent with previous studies (Ford 1991; Yurk et al. 2002) I found no new call types had been invented or innovations on old call types had occurred and call type structure had not perceptually changed. I found that some rarely used call types were recorded in one time period, but not the other as reported previously by Ford (1991) and Yurk et al. (2002).

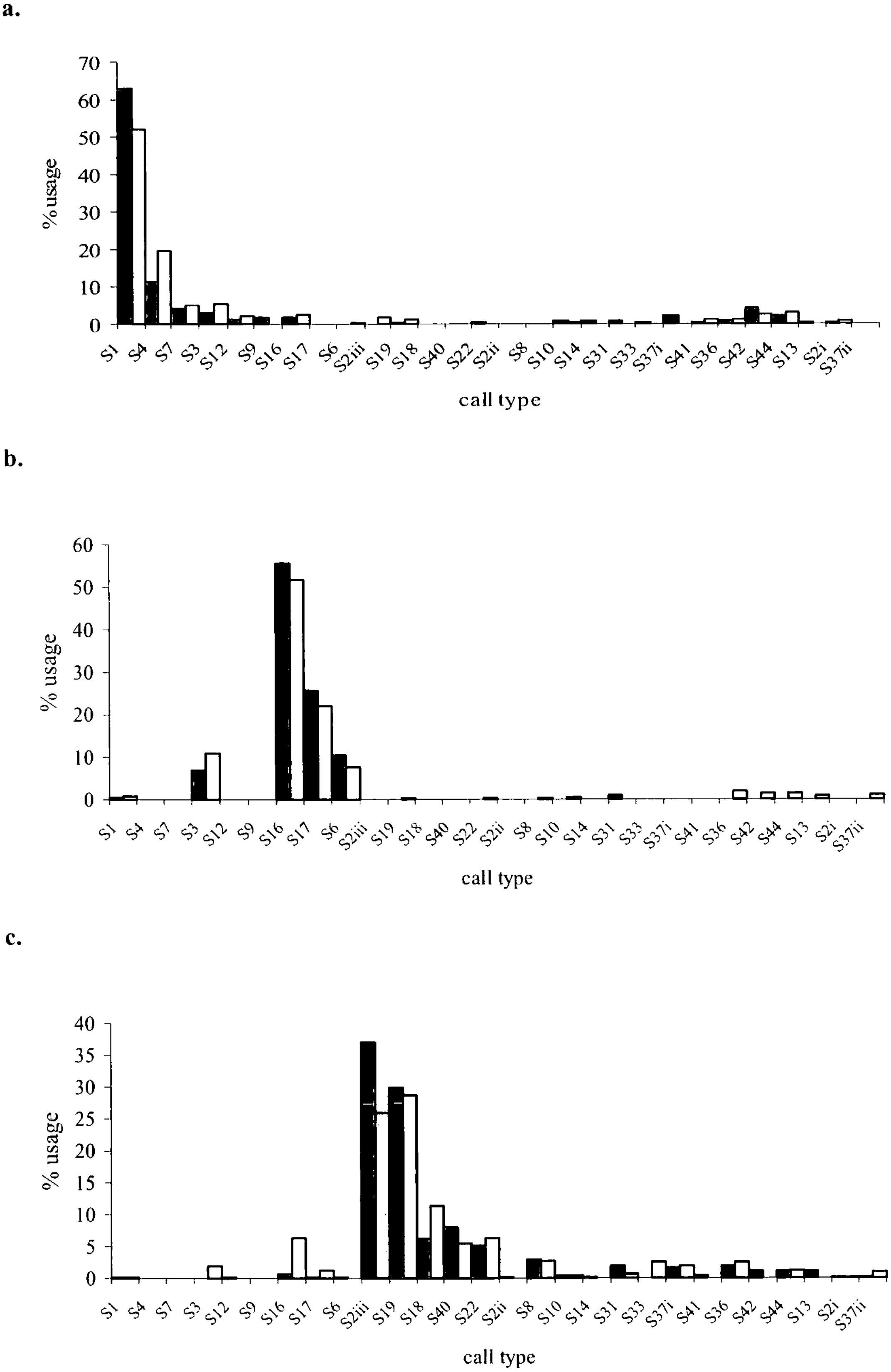
Although each pod shared a number of call types with the other two, the proportional usage was highly distinctive from the other two pods in both time periods (figure 3.1). The proportional usage of each call type by each pod was strongly correlated between both time periods (Pearson's product moment correlation for J pod: $r_{25} = 0.979$, $N_1 = 993$ calls, 23 recording sessions, $N_2 = 767$ calls, 35 recording sessions, $P < 0.001$; K pod: $r_{16} = 0.991$, $N_1 = 230$ calls, 6 recording sessions, $N_2 = 441$ calls, 17 recording sessions, $P < 0.001$; L pod: $r_{23} = 0.956$, $N_1 = 1403$ calls, 13 recording sessions, $N_2 = 672$ calls, 26 recording sessions, $P < 0.001$; figure 3.2). This suggests that there is overall stability in the proportional usage of call types within each pod's repertoire, however the correlation results may be inflated by one or two outlying data points for J and L pods (figure 3.2).

A comparison of the mean relative usage per recording session of the two most common call types produced by each pod also found no significant difference between each time period (Table 3.1). Mann Whitney U test: J pod, call type S1: $U = 195.0$, $P = 0.287$; call type S4: $U = 188.0$, $P = 0.410$; K pod, call type S16: $U = 40.0$, $P = 0.313$; call type S17: $U = 33.0$, $P = 0.792$; L pod, call type S19: $U = 154.0$, $P = 0.072$; S2iii: $U = 111.0$, $P = 0.983$.

Pod	Call type	Number of that call type recorded (1977-1981)	Mean relative usage per recording session (%)	Number of that call type recorded (2001-2003)	Mean relative usage per recording session (%)	**P**
J	S1	623	55.6	400	45.0	0.287
J	S4	150	8.7	110	19.7	0.410
K	S16	128	66.8	190	44.5	0.313
K	S17	59	19.6	81	17.34	0.792
L	S19	420	38.1	193	23.4	0.072
L	S2iii	519	27.8	174	26.9	0.983

Table 3.1 The mean percentage of the total call production represented by the two most common call types of each pod within each time period.

Figure 3.1 A comparison of call type usage between two time periods ■: 1977-1981 and □: 2001-2003 by: **a.** J pod; **b.** K pod; **c.** L pod.



Discussion

Each of the three Southern Resident pods was acoustically distinctive and their proportional call usage between time periods was strongly correlated (figure 3.1). The lack of any observed immigration into any of the focal killer whale pods during the time period spanned by my recordings (Van Ginneken et al. 2005) could contribute to the stability of pod specific call type repertoires (Ford 1991). In chapter 2 I found an orphaned L pod killer whale predominantly using J pod's main call type, suggesting that resident killer whales do learn the common call types from other pods, but that usage learning keeps each pod's repertoire distinct. It seems unlikely that one call type repertoire would have a significant functional advantage over another (although some call types differ in transmission properties, see chapter 4). There is therefore no reason for one pod not to adopt another's call type repertoire unless kin recognition is an important function of call types.

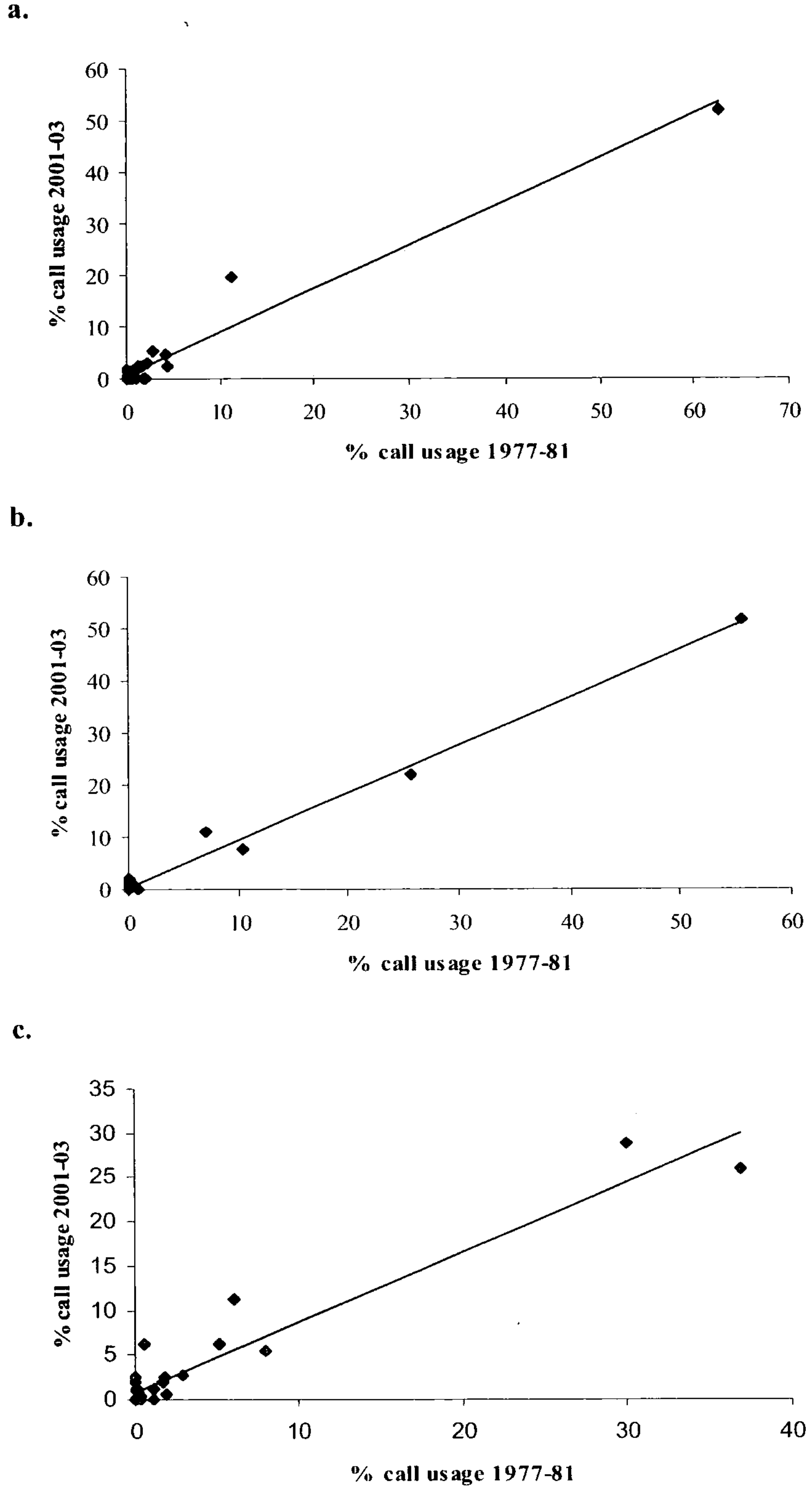
However, much of the support for the correlations I found was due to the most frequently produced call types, which are distinct among pods (see figure 3.1). Therefore a subset of redundantly produced call types may be serving to establish pod identity, though additional function for these call types cannot be ruled out from my data. Other call types within a pod's repertoire that were produced rarely appeared less strongly correlated over time and may be less important for group recognition. Differences in transmission properties between call types within each pod's repertoire imply differences in the functional or contextual use (Hoelzel and Osborne 1986; Miller 2002, 2006), this is further supported by contextual correlates based on transmission properties (chapter 4).

It has been suggested that social learning and conformist transmission of cultural traits may have been selected for social identification due to the benefits of group membership (Boyd and Richerson 1985; Henrich and Boyd 1998; Nettle 1999; Lachlan et al. 2004). Conformity can also be enforced by the punishment of non-conformists (Boyd and Richerson 1992; Henrich and Boyd 1998; Lachlan et al. 2004). An increase in affiliative interactions and a decrease in aggression in American crow *Corvus brachyrynchos* groups concurrent with vocal convergence were noted by Brown (1985). An array of kin-directed and cooperative behaviour has been noted in killer whales, e.g. allo-parenting, cooperative foraging and prey sharing (Haenel 1986; Waite 1988; Hoelzel 1991, 1993; Guinet et al. 2000), however aggression has rarely been observed (Ford et al. 2000). Selection could therefore act on the individual and promote conformist behaviour and call sharing between individuals within a pod but maintaining a repertoire distinctive from other pods within the population. Non-conformists may risk being separated from the natal pod removing the benefits of group living and possibly increasing aggressive interactions, thereby reducing survivorship.

Unlike bottlenose dolphins, which have individually distinctive signature whistles adapted for individual recognition in a fission-fusion social structure (Caldwell et al. 1991), the importance of group identity in the stable social structure of killer whales may be more important than individual identity (Nousek 2004).

promote conformist behaviour and call sharing between individuals within a pod but maintaining a repertoire distinctive from other pods within the population. As non-conformists may risk being separated from the natal pod removing the benefits of group living and possibly increasing aggressive interactions, thereby reducing survivorship. Unlike bottlenose dolphins, which have individually distinctive signature whistles adapted for individual recognition in a fission-fusion social structure

Figure 3.2 A plot of proportional usage of each call-type in 1977-1981 against 2001-2003 by: **a.** J Pod; **b.** K Pod; **c.** L pod.



(Caldwell et al. 1991), the importance of group identity in the stable social structure of killer whales may be more important than individual identity (Nousek 2004).

Many species distinguish between kin and non-kin using individually distinctive differences in the structure of shared call types (e.g. rhesus monkeys *Macaca mulatta* Rendall et al. 1996; long-tailed tits *Aegithalos caudatus* Sharp et al. 2005). These differences can be caused by the shape of the vocal tract and sound production organs (e.g. Rendall et al. 1998). In cetaceans these small involuntary differences may be lost due to the effects of pressure on the gas filled cavities at different depths (Janik and Slater 2000; Tyack 2000). This seems unlikely to affect the frequency contours of pulsed killer whale call types in which fundamental frequency is a product of the pulse rate (Schevill and Watkins 1966), but may still affect any individuality in the energy distribution of the harmonics which may be determined by the size of the resonance chambers.

Cues for kin recognition in signal structure can also be the result of matching call structure during the learning process if kin are in close association during vocal development (e.g. Sharp et al. 2005). Killer whale shared call types are structurally individually distinctive (Hoelzel and Osborne 1986; Nousek 2004), which suggests that a single call type may be sufficient for individuals to be able to recognise close kin. However inter-individual differences in call structure are much smaller than inter-matriline differences (Nousek 2004) and it has not been demonstrated that killer whales can or do discriminate between individuals or matrilines using these subtle structural differences. Structural similarity of call types is maintained between closely associating individuals and groups due to call type structural matching (Deecke et al. 2000; Nousek 2004) leading to a positive correlation between structural similarity and level of association (Deecke 1998; Miller and Bain 2000). Additionally these small structural differences may be masked over the large distances that pods frequently spread out, due to the high level of reverberation and scatter in the marine environment (Urick 1983). These factors reduce the effectiveness of using structural differences of a shared call type to discriminate between closely associating groups such as J, K and L pods. Kin recognition may be more effectively achieved by distinctive frequency-modulated group-specific call types, which are slow to change over time.

Boughman and Wilkinson (1998) found in a playback study that greater spear-nosed bats discriminated group mates that shared a group specific call from other groups in the same roosting cave, but did not appear to discriminate between individuals from within their own group. A similar experimental approach could identify if killer whales discriminate between pods, matrilines or individuals and the relative importance of proportional call type usage and call structure in achieving this.

Chapter 4 - Social and behavioural correlates of two-component call type usage.

Introduction

Many species of mammals live in murky marine or densely forested habitats, are nocturnal or are separated from conspecifics over large distances. For these species sound is an important modality for long-range communication and they have evolved vocalisations to maintain contact between individuals and groups and coordinate their movements (e.g. African elephants *Loxodonta africana* McComb et al. 2000, 2003; greater spear-nosed bats *Phyllostomus hastatus* Wilkinson and Boughman 1998; red-bellied tamarins *Saguinus labiatus* Caine and Stevens 1990; spinner dolphins *Stenella longirostris* Lammers and Au 2003). These signals are expected to be audible over the necessary spatial scales, but will be degraded between the signaller and the receiver in several ways; absorption, amplitude degradation, frequency dependent attenuation, reflection, reverberation, scattering and spherical spreading (Wiley and Richards 1982; Urick 1983). The frequency range and bandwidth of a signal can determine its transmission properties e.g. low frequency, narrowband sounds propagate further in most habitats (Wiley and Richards 1982). The transmission properties of a signal often determine the contexts in which it is used. Signals with a lower active space are often used between individuals in close contact and those with a higher active space are used when signaller and receiver are separated over longer distances, e.g. the intra-group and inter-group calls of the grey-cheecked mangabey *Cercocebus albigena* (Waser 1975; Waser and Waser 1977) and pygmy marmosets *Cebuella pygmaea* (De La Torre and Snowdon 2002).

The mechanisms of how groups of individuals use these calls to coordinate their movements is less well understood, although recent studies have suggested that receivers may use cues in the structure of a call which result from transmission loss due to attenuation or signal directionality to judge the signaller's distance (Naguib and Wiley 2001), azimuth and elevation (Nelson and Stoddard 1998) and direction of movement (Miller 2002; Lammers and Au 2003).

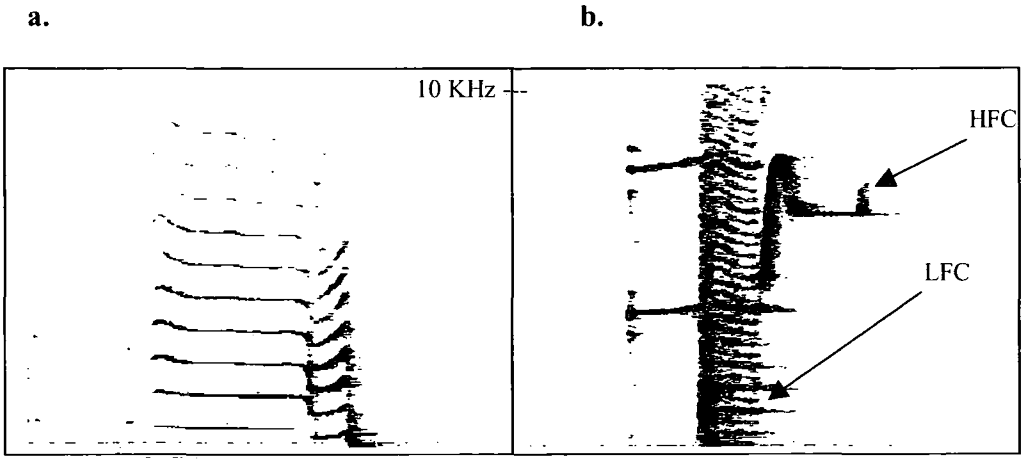
The Southern Resident population of killer whales is found in the nearshore waters of Washington State and British Columbia and consists of three matrifocal pods; J, K and L. Pods can be further split into sub-pods and intra-pod groups commonly and hereafter in this chapter referred to as matrilines (Bigg et al. 1990). Inter-pod associations are characteristic of a fission-fusion social structure and associations between pods can change over periods of hours (Bigg et al. 1990). It is thought that the calls function in maintaining contact between group members (Ford et al. 1989, 1991; Miller 2000) and coordination during foraging (Hoelzel and Osborne 1986) although these mechanisms are still poorly understood. Call type usage varies across broad behavioural categories but no specific call has yet been exclusively associated with one type of behaviour (Bain 1986; Hoelzel and Osborne 1986; Morton et al. 1986; Ford 1989).

Each call type consists of a low frequency component (LFC) thought to be produced by rapid pulses resulting in a tone like structure with harmonics at intervals equal to the pulse repetition rate (Schevill and Watkins 1966; figure 1a) ranging to over 30 kHz when recorded on axis (Miller 2002). This component is relatively omni-directional up to 5 kHz, but harmonics above 5 kHz increase in directionality with increasing frequency (Miller 2002). Some call types also contain an overlapping tonal high frequency component (HFC), with a structure completely unrelated to the LFC which has a fundamental frequency of between 2-12 kHz (Hoelzel and Osborne 1986; Ford 1987; Bain and Dahlheim 1994; Miller and Bain 2000) and harmonics ranging to over 100 kHz (Bain and Dahlheim 1994; figure 1b). Although the beam angle has not been measured, the HFC has been shown to be highly directional and have a forward facing beam pattern (Bain and Dahlheim 1994; Miller 2002). Miller (2002) compared the relative energy distribution in two frequency bands (0-5 kHz and 5-14 kHz) and found a significant difference between call types with an HFC recorded when the whale was facing the hydrophone to those recorded when the whale was facing away. There was no significant difference in the relative energy distribution with direction of the whale for single-component call types (Miller 2002). He hypothesized that killer whale receivers could use the relative strength of the HFC and LFC resulting from the effects of mixed directionality to determine the direction of movement of the signaller (Miller 2002).

The HFC can contain more energy than the LFC (Bain and Dahlheim 1984), and Miller (2006) found two-component call types have a higher source level and a higher estimated active space (10-16 km) compared with single component call types (5-9 km). On this basis Miller (2006) suggested that call types would be separated into short and long range calls by whether they contained a HFC or not. He proposed that single-component call types could be used preferentially in intra-pod interactions and two-component call types when pods meet in large aggregations (Miller 2006)

In this chapter I investigate usage of two-component call types by the Southern Resident population of killer whales. I compare recordings of individual pods travelling directionally with recordings of individual pods during 180° group direction change and recordings of single pods with those of multiple pods.

Figure 4.1 Spectrograms of **a.** a single component call type and **b.** a two-component call type (Filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752ms and 21.73 Hz).



Method

See chapter 2 for recording and acoustic analysis method and materials.

I compared the mean proportional usage per recording session of two-component call types between pods and between recordings of each pod during directional travel with those in which the pod changed direction 180° using a Mann Whitney *U* test.

I compared the usage of two-component call types from recordings of all three pods together between the contexts of the pods converging, social behaviour and non-social travel. Converging was defined as the period 10 minutes before and 10 minutes after all three pods come into contact with one another. Socialising was defined as when all or most individuals were involved in tactile interactions and surface-active behaviours and non-social travel was defined as directional movement in which no sub-group or individuals were involved in body rubbing or surface-active behaviours. Recordings that did not strictly fit into one of these three behavioural categories were excluded. A Mann-Whitney *U* test was used to compare the mean relative usage of two-component call types between each context.

Results

See chapter 2 for the number of recording sessions and call types categorised.

L pod used a significantly higher mean proportion of two-component call types per recording session than either J pod (Mann-Whitney *U* test: $U = 1537.0$, $P < 0.0001$), or K pod (Mann-Whitney *U* test: $U = 938.0$, $P < 0.0001$; table 4.1; figure 4.3).

There was no significant change in the mean percentage usage of two-component call types per recording session during recordings of each pod changing direction of movement 180 ° compared to directional travel (Mann-Whitney *U* test: J pod, $U = 107.0$, $P < 0.308$; K pod, $U = 58.5$, $P = 0.113$; L pod, $U = 116.5$, $P = 0.467$). Figure 4.3 shows the proportional call type usage of each pod during directional travel and during 180° group direction changes and which of these are two-component call types.

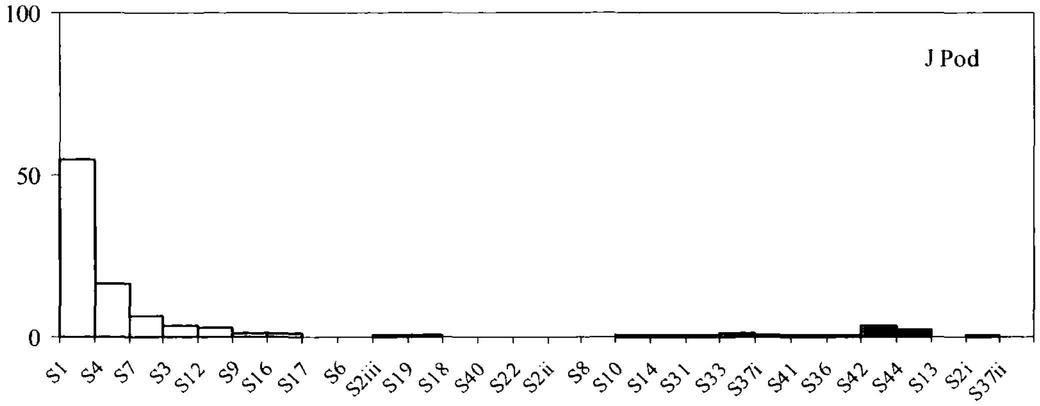
The proportional usage of two-component call types were significantly greater in recordings of all three pods together during a convergence (Mann-Whitney *U* test: $U = 29.0$, $P = 0.0448$) and during social behaviour (Mann-Whitney *U* test: $U = 57.0$, $P = 0.00262$) than during non-social travel. I could not determine to what extent these differences were due to increased representation by L pod in recordings of converging and socialising, the high use of call types of S19 and S2iii suggest this may be a factor, however the high use of call type S36 during these recordings, a call type not commonly when L pod was recorded alone, suggests that context is also important. There was no significant change in the mean percentage usage of two-component call types per recording session between recordings of J, K and L pod during a convergence than during social behaviour (Mann-Whitney *U* test: $U = 15.0$, $P = 0.464$).

I also recorded two lone K pod whales (K11 and K31) on two different occasions separated by several kilometres for several hours in one case and several days in another from K pod, using predominantly (87.5%) two-component call types. These individuals used a part of the same subset of call types (S13, S36 & S37ii) used in multi-pod recordings and neither individual produced K pod's most common call types (Figure 3), however the sample size was small (51 calls, 2 recording sessions).

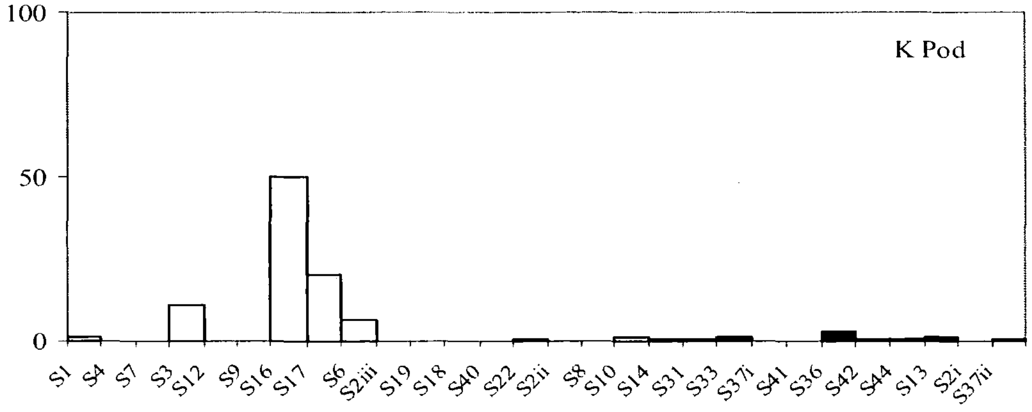
Pod(s)	Total number of stereotyped calls	Number of recording sessions	Total recording time (mins)	Mean relative usage of two-component call types per recording session (%)
J	2588	59	1475	16.0
J – direction change	86	5	151	50.0
K	866	34	1050	8.8
K – direction change	161	4	169	28.1
L	2612	49	1288	85.0
L – direction change	224	6	231	88.8
J, K	2918	41	1147	11.0
J, L	457	8	294	70.9
K, L	330	11	302	49.1
J, K, L	4510	33	1331	65.2
J, K, L – non-social travel	666	10	189	38.1
J, K, L – pods converge	733	5	98	81.2
J, K, L – socializing	1175	8	182	91.5

Table 4.1 Percentage of two-component call types from recordings of each pod (during directional travel and direction change) and multi-pod combination (during different contexts for J, K & L).

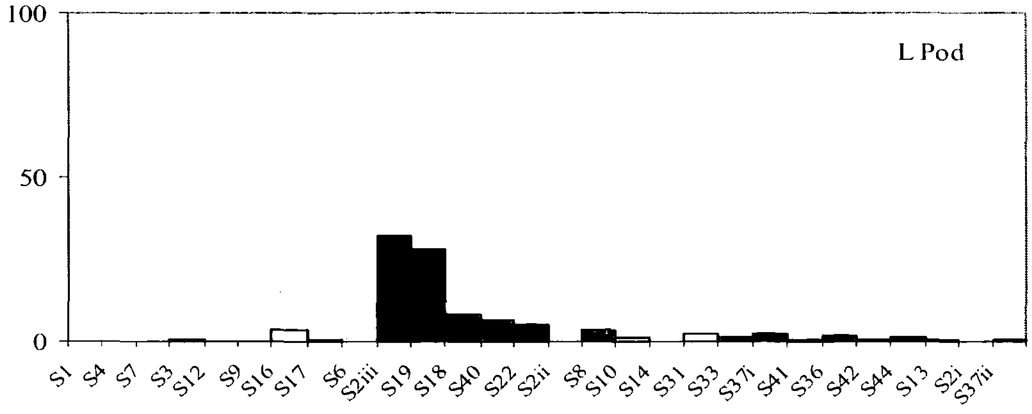
a.


100
50
0
J Pod
S1
S4
S7
S3
S12
S9
S16
S17
S6
S2iii
S19
S18
S40
S22
S2ii
S8
S10
S14
S31
S33
S37i
S41
S36
S42
S44
S13
S2i
S37ii

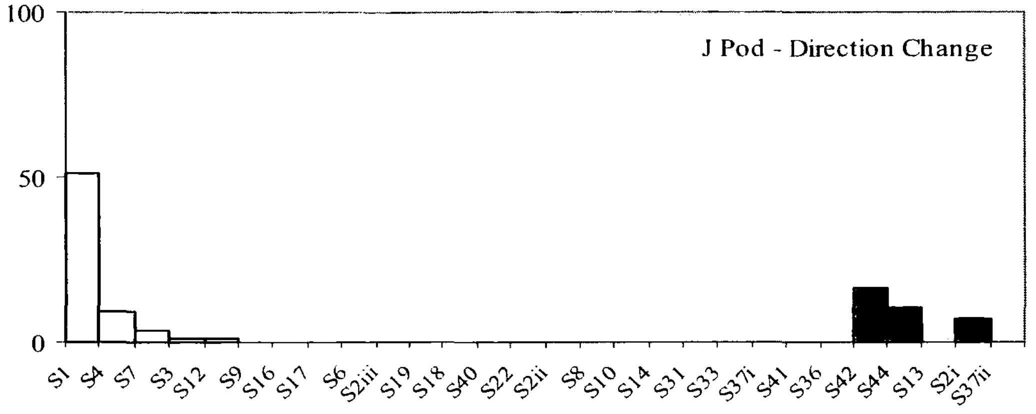
b.


100
50
0
K Pod
S1
S4
S7
S3
S12
S9
S16
S17
S6
S2iii
S19
S18
S40
S22
S2ii
S8
S10
S14
S31
S33
S37i
S41
S36
S42
S44
S13
S2i
S37ii

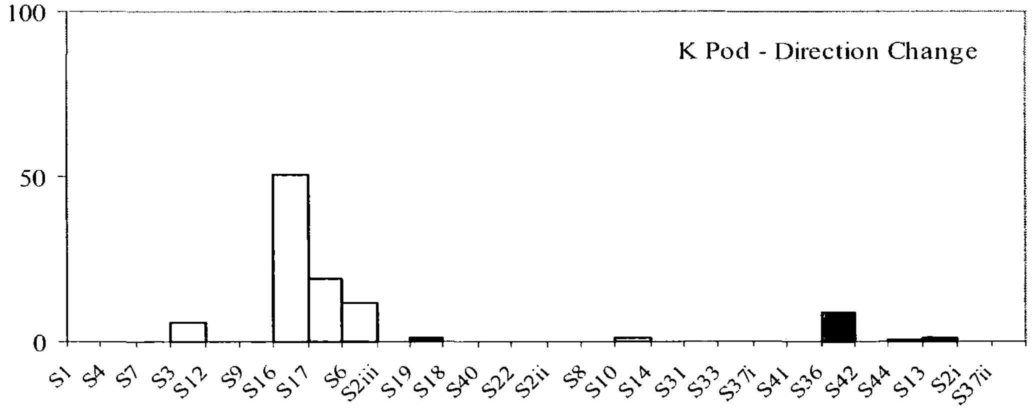
c.


100
50
0
L Pod
S1
S4
S7
S3
S12
S9
S16
S17
S6
S2iii
S19
S18
S40
S22
S2ii
S8
S10
S14
S31
S33
S37i
S41
S36
S42
S44
S13
S2i
S37ii

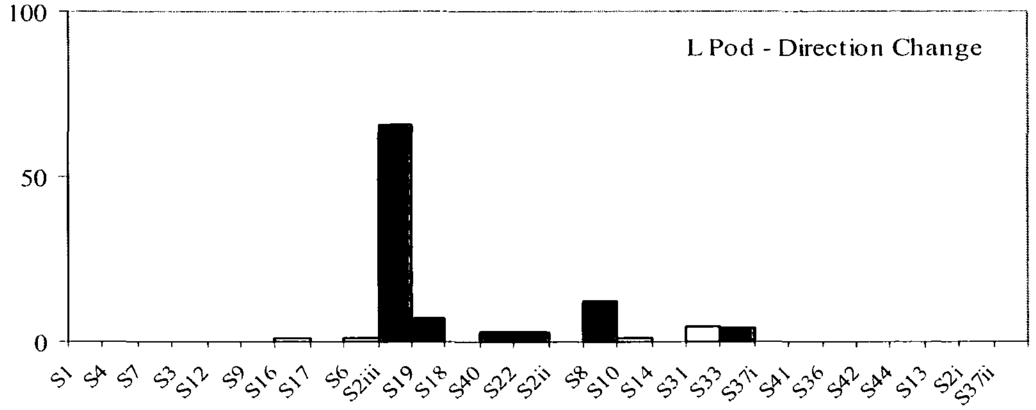
d.


J Pod - Direction Change
100
50
0
S1 S4 S7 S3 S12 S9 S16 S17 S6 S2iii S19 S18 S40 S22 S2ii S8 S10 S14 S31 S33 S37i S41 S36 S42 S44 S13 S2i S37ii

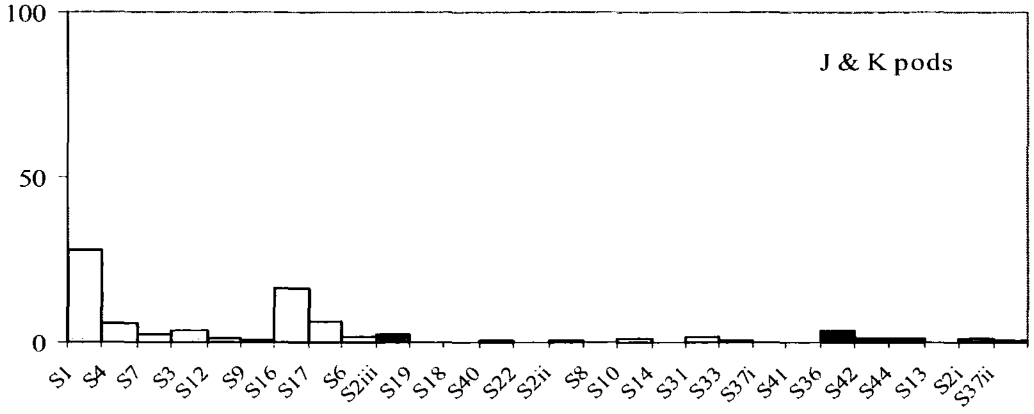
e.


K Pod - Direction Change
100
50
0
S1 S4 S7 S3 S12 S9 S16 S17 S6 S2iii S19 S18 S40 S22 S2ii S8 S10 S14 S31 S33 S37i S41 S36 S42 S44 S13 S2i S37ii

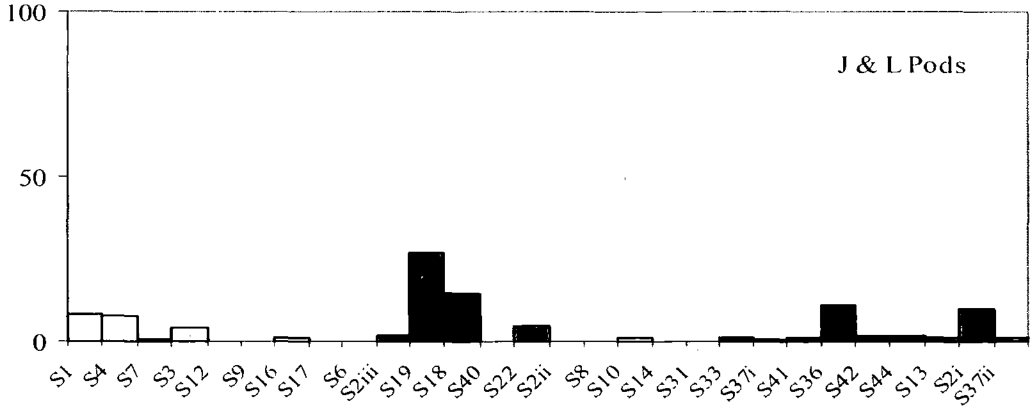
f.


L Pod - Direction Change
100
50
0
S1 S4 S7 S3 S12 S9 S16 S17 S6 S2iii S19 S18 S40 S22 S2ii S8 S10 S14 S31 S33 S37i S41 S36 S42 S44 S13 S2i S37ii

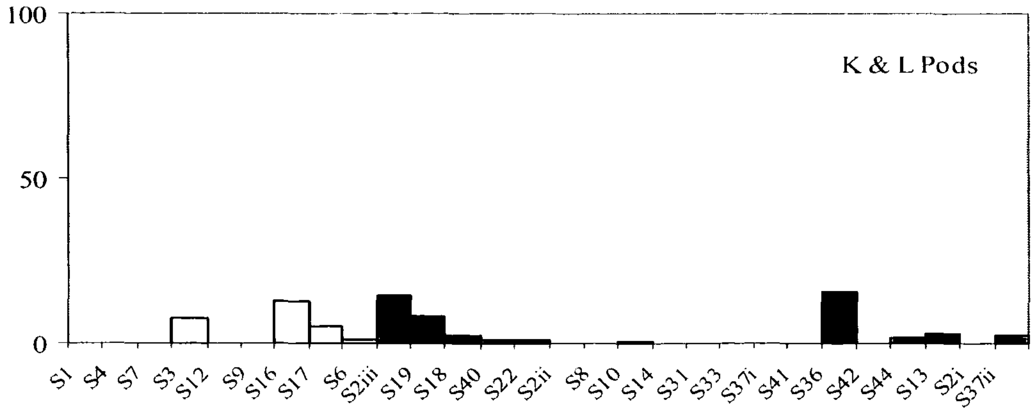
g.


100
50
0
J & K pods
S1 S4 S7 S3 S12 S9 S16 S17 S6 S2iii S19 S18 S40 S22 S2ii S8 S10 S14 S31 S33 S37i S41 S36 S42 S44 S13 S2i S37ii

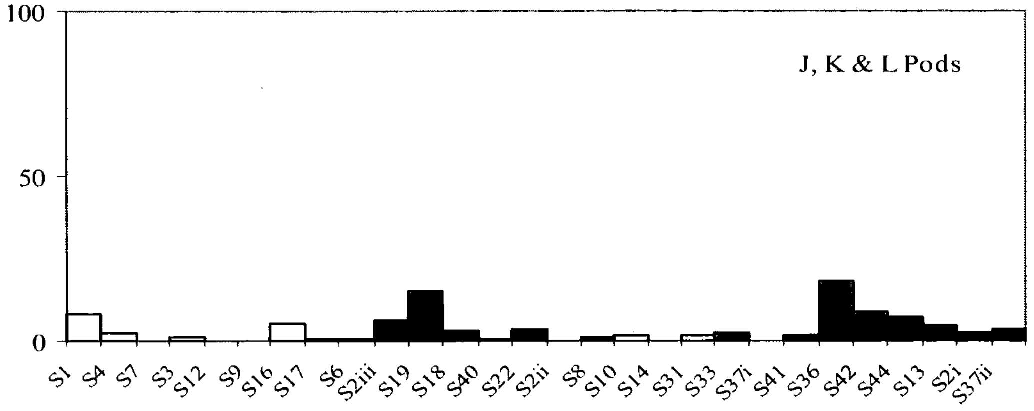
h.


100
50
0
J & L Pods
S1 S4 S7 S3 S12 S9 S16 S17 S6 S2iii S19 S18 S40 S22 S2ii S8 S10 S14 S31 S33 S37i S41 S36 S42 S44 S13 S2i S37ii

i.


100
50
0
K & L Pods
S1 S4 S7 S3 S12 S9 S16 S17 S6 S2iii S19 S18 S40 S22 S2ii S8 S10 S14 S31 S33 S37i S41 S36 S42 S44 S13 S2i S37ii

j.



k.

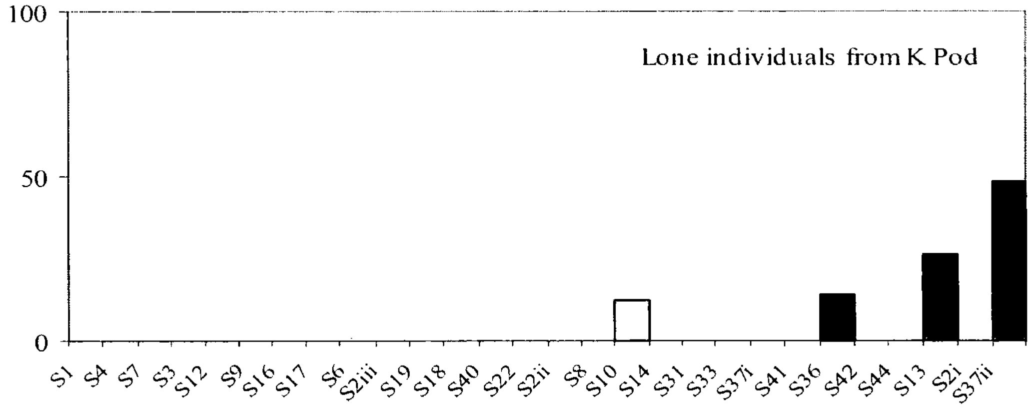


Figure 4.2 Proportional call type usage (%) of each pod during directional travel: **a.** J pod; **b.** K pod; **c.** L pod; during 180 group direction changes **d.** J pod; **e.** K pod; **f.** L pod; multi-pod combination: **g.** J & K pods; **h.** J & L pods; **i.** K & L pods; **j.** J, K & L pods; and **k.** lone individuals K11 & K31.

□: Single-component call types; ■: Two-component call types.

Discussion

Miller (2002) had hypothesised that killer whale receivers may use the relative strength of the LFC and HFC components resulting from mixed directionality as a cue to the direction of movement of the signaller. I did not find a significant increase in the proportion of two-component call types by any of the three pods during a change of direction to support this hypothesis. However two-component call types dominated L pod's call type usage (91%), even when travelling directionally and so individuals could still be using mixed-directionality as a direction of movement cue. Direction changes can take over 30 minutes for all members of a pod to complete and it may take only a single individual to signal a direction change at the start of this process, resulting in only a small increase in the proportional usage of two-component call types in recordings of the whole process possibly explaining why I did not detect any significant change in call usage by K pod. Recordings of identified individuals using multi-hydrophone arrays (see Miller and Tyack 1998) are needed to further test this. Alternatively killer whales may simply use binaural discrimination or even non-vocal acoustic cues to detect direction changes by the rest of the group. Group direction changes are frequently preceded by percussive behaviours by individuals at the trailing end of the group, who then start the change of direction (Felleman 1986; personal observation). Playbacks may be a more effective test of whether killer whales, or other species that produce signals with mixed directionality, such as spinner dolphins, which produce whistles with harmonics that increase in directionality with increasing frequency (Lammers and Au 2003), actually do attend to structural cues to judge the directionality of the signaller (Miller 2002).

A subset of two-component call types recorded infrequently by each pod when recorded individually were recorded frequently in multi-pod recordings (figure 4.3). Ford (1989) previously found that the N2 two-component call type, the call type with the highest estimated active space of the nine call types for which source level was measured (Miller 2000), increased when Northern Resident population A-clan pods met.

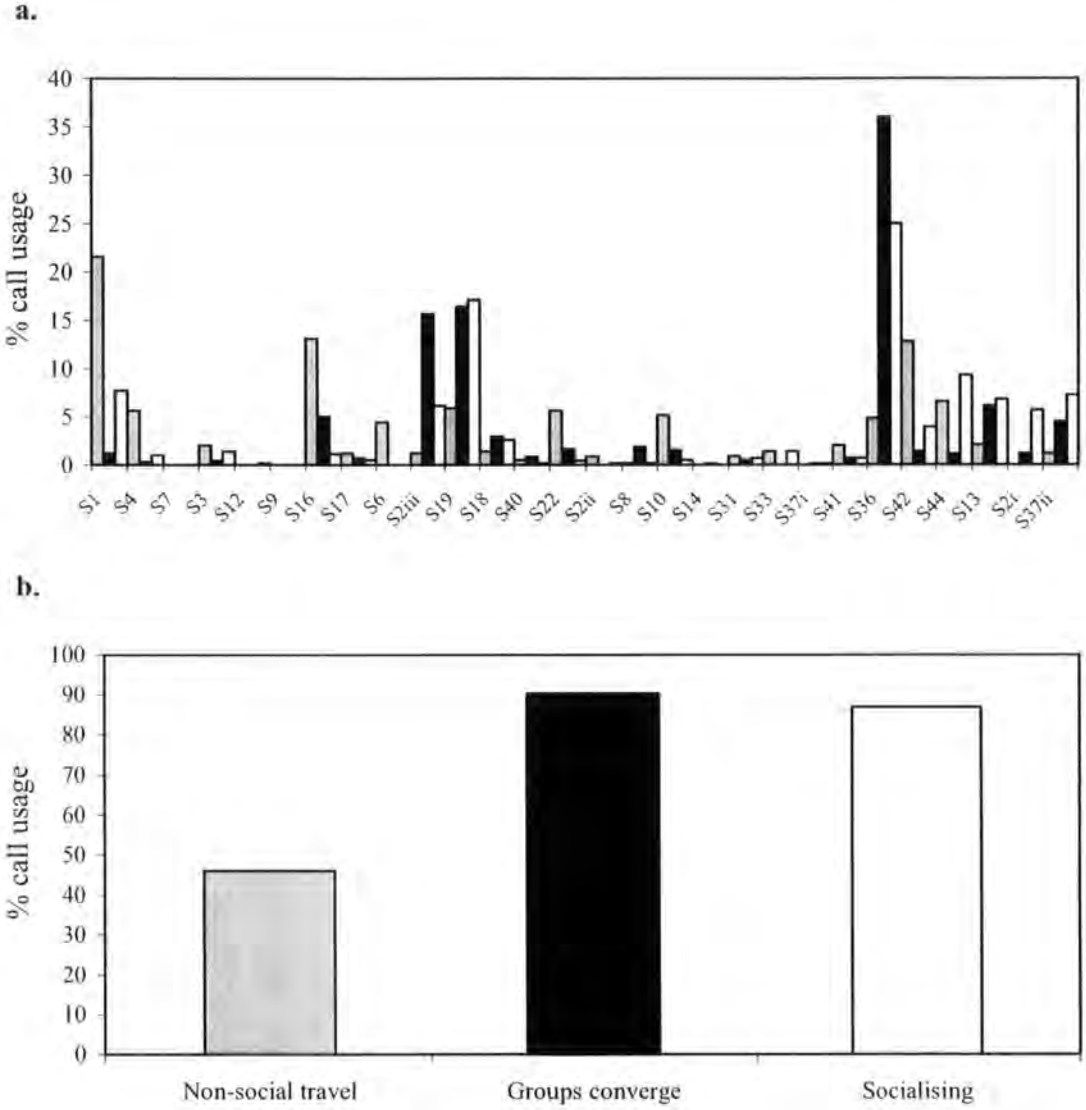


Figure 4.3a. Proportional usage of call types and **b.** percentage of two-component call types recorded from multi-pod aggregations of J, K and L pods during: non-social travel; • group convergence and; • social behaviour.

It could be that two-component call types are associated with social behaviour, which occurs more frequently in multi-pod groups than single pods (Osborne 1986). Bain (1986) found a correlation between levels of arousal and call type usage in captive Northern Resident A-clan killer whales with the N2 call type being given in higher arousal states. Miller (2000) suggested that signallers could use the directionality of the HFC to direct the call at a particular receiver; this could also be a function that would be useful in multi-pod aggregations, when most mating takes place (Barrett-Lennard 2000).

However L pod use a significantly higher proportion of two-component call types than either J or K pod (11% and 8% respectively) (table 4.1; figure 4.2), but do not engage in social activity more frequently than the other two pods (Osborne 1986) and use two-component call types across a wide range of contexts (Hoelzel and Osborne 1986; Ford 1989). L pod, (approx 40 individuals), is approximately twice as large as J and K pods (approx 20 individuals each) (Bigg et al.1990; Ford et al. 2000; Van Ginneken et al. 2000). L pod also contains more matrilines (15) than J and K pods (5 each) and based on a point correlation coefficient, L pod has a lower level of association between its matrilines than J and K pods (Bigg et al. 1990). This lack of pod cohesion in the L pod matrilines means calls often need to be detected over greater distances to maintain contact between and reunify matrilines than for J and K pods. The higher active space of two-component call types means they would be more effective at achieving this than single-component call types.

This also appears the most parsimonious, but non-exclusive explanation for the observed increase in usage during inter-pod interactions, because they have a higher active space than single-component call types and are therefore better suited for long-range detection by other pods (Miller 2000). However the use of long-range, highly localisable call types may indicate a willingness to interact and mediate a convergence and socialising between pods.

Additionally two lone K pod individuals separated from the pod on separate occasions by several kilometres for several hours also used predominantly two-component call types rather than the single component primary call type of K pod. Saulitis et al. (2005) similarly found that lone AT1 transients or groups prior to a convergence used a subset of high amplitude call types. Groups were seen apparently responding to these calls from over 9 km away (Saulitis et al. 2005). Two of these call types were two-component call types, while the third was almost exclusively given immediately before one of the two-component call types (Saulitis et al. 2005). All other call types in the AT1 transient repertoire were single-component call types (Saulitis et al. 2005).

Focusing the energy of a sound into a narrowband, directional beam can increase its transmission properties if the receiver is on axis (Wiley and Richards 1982; Brown 1982). Spectrograms of calls with a high amplitude always contain at least the fundamental and harmonics up to 2 kHz of the LFC, (the HFC can sometimes be missing due to the call being recorded off axis, see Miller 2002). Spectrograms of calls recorded with a low amplitude, presumably due to the distance between the whales and hydrophone, sometimes contain the HFC, but only a faint LFC, (Figure 4.5). This confirms that, at least in certain sound propagation conditions, the HFC can propagate further than the LFC when recorded on axis.

Selection of narrowband, long distance calls and broadband, close range calls has been found in species from highly reverberant environments such as dense forests, e.g. mangabeys (Waser 1975; Waser and Waser 1977), macaques (Brown et al. 1979; Brown 1982) and pygmy marmosets (De La Torre and Snowdon 2002). Lohr et al. (2003) found that narrow band canary calls had lower detection thresholds than broadband zebra finch calls in budgerigar *Melopsittacus undulatus* and zebra finch *Taeniopygia guttata* receivers.

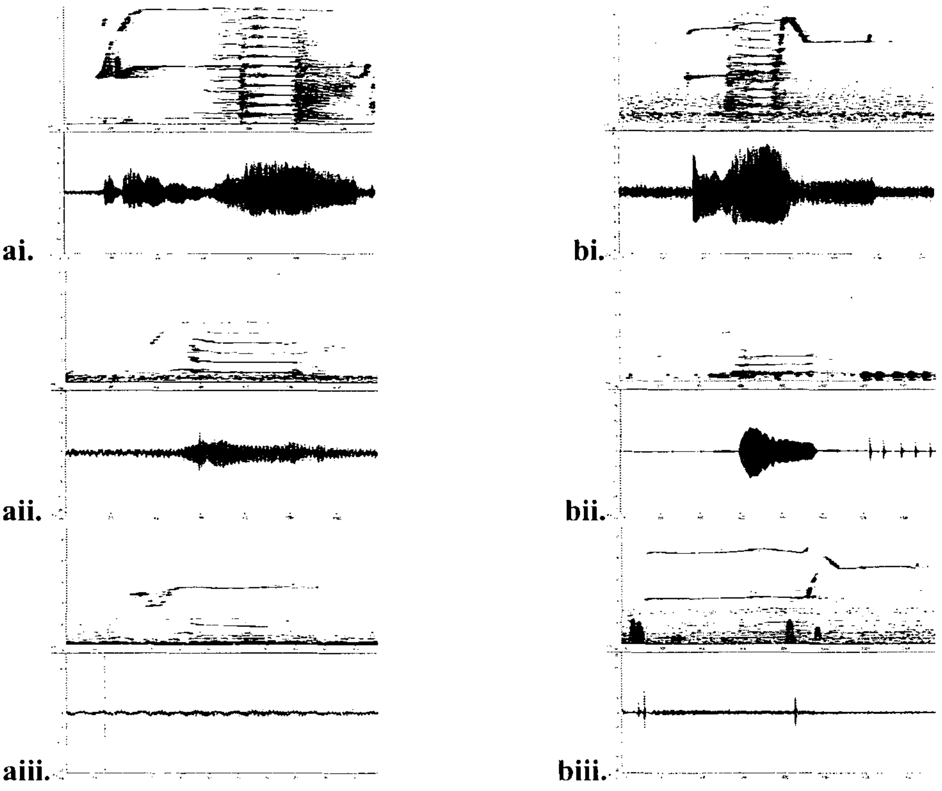


Figure 4.5 Spectrograms (Filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752ms and 21.73 Hz) and waveforms of **a.** call type 24 and **b.** call type 25 showing **i.** high amplitude, pulsed LFC and tonal HFC, **ii.** high amplitude, pulsed LFC, tonal HFC absent, **iii.** low amplitude, tonal HFC, pulsed LFC absent.

Many terrestrial species use lower frequency sounds for long distance communication to avoid frequency dependent attenuation by absorption that is relatively high in air, e.g. mangabeys (Waser 1975; Waser and Waser 1977) and African elephants (McComb et al. 2000; 2003). Some baleen whale species e.g. fin whales *Balaenoptera physalus* use infrasonic signals and are thought to be able to communicate over distances of hundreds of kilometers (Watkins 1987). However the increase in absorption loss levels in seawater at the frequency of the fundamental of the HFC (2-12 kHz) compared to the fundamental of the LFC (80-2400 Hz) would be negligible over the active space of a killer whale call (8-15 km)(Clay and Medwin 1977). Therefore it may not be advantageous to use lower frequencies (<1 kHz) for long distance communication in the marine environment in a species whose hearing is more sensitive to higher frequencies (Szymanski et al. 1999) and which are only likely to be acoustically interacting over tens of kilometres (Miller 2000).

Although I could not find a correlation between group direction changes and the use of two-component call types for all three pods, the high usage of these call types in inter-pod interactions may be connected to the mixed-directionality of components. Receivers could use the beam angle of the highly directional, tonal HFC to judge the azimuth of the signaller and guide them to meet head on. Receivers may also be able to use the different propagation properties of each component to judge the distance of signallers. For example at distances of 10 km frequency dependent absorption would cause a loss of approximately15dB more for harmonics of the HFC at 20 kHz than those at 10 kHz (Au et al. 2000). The relative strength of the LFC and the level of reverberation would inform the receiver if these differences were due to the directionality or distance of the signaller providing they were familiar with the signal at source (Miller 2002).

Ford (1989) found that a call type is usually sequentially followed by the same call type, Miller et al. (2004) were able to demonstrate that this was often due to anti-phonal call type matching between individuals within a matriline and not repetition by the same individual. A subset of two-component call types were found in the repertoire of each pod when recorded individually and occurred in each one of the two pod comparisons suggesting that at least two of the pods were responsible for the high usage of these call types in multi-pod aggregations. Therefore call type sharing and matching may also be important to inter-pod as well as intra-pod interactions. The N2 call type used during inter-pod interactions (Ford 1989) is also the only call type not found to be matrilineally structurally distinct by Miller and Bain (2000) suggesting that structure is matched between groups by horizontal transmission (see Deecke et al. 2000)

Signal matching occurs in bottlenose dolphins *Tursiops truncatus* (Janik 2000a) and many songbirds (e.g. great tits *Parus major* Peake et al. 2005; song sparrows *Melospiza melodia* Beecher et al. 2000). Call type matching and sharing may be important as detailed knowledge of the call's structure at source may aid a receiver in using structural cues due to attenuation and mixed directionality of components to make a reliable judgment of distance, azimuth, elevation and direction of movement of the signaller (Morton 1986; Miller 2000; Naguib and Wiley 2001; Miller et al. 2004, but see Naguib 1997; Wiley 1998). Further investigations using multi-hydrophone arrays are needed to determine if pods sequentially match call types during inter-pod vocal exchanges (see Miller et al. 2004).

It appears that the call type repertoires of resident killer whales contain both exclusive intra-pod calls and shared inter-pod contact calls. Several species of flocking birds that form long-term relationships and stable groups e.g. Australian magpies *Gymnorhina tibicen*, American crows *Corvus brachyrhynchos*, budgerigars *Melopsittacus undulatus* and European starlings *Sturnus vulgaris* (Brown and Farabaugh 1997; Hausberger 1997) show a similar pattern of hierarchical song or call sharing. Song or call types can be shared at species, population, group and mated pair level whilst others are unique to the individual (Brown and Farabaugh 1997; Hausberger 1997). Resident killer whale call type repertoire appear to reflect the multi-layered social structure and probably facilitate the interactions that occurs within each layer, e.g. allo-parenting and food provisioning within a matriline (Waite 1988; personal observation), coordinated foraging within a pod (Hoelzel 1993) and social and mating behaviour between pods (Osborne 1986; Barrett-Lennard 2000).

Chapter 5 - Anti-masking response to anthropogenic noise.

Introduction.

Many species face the challenge of signal detection and discrimination against a background of vocalisations from con- and hetero-specifics, known as the cocktail party effect (Cherry 1966), ambient noise caused by the environment, e.g. wind, waves and rain (see chapter 6), and anthropogenic noise. Ambient and biotic noise have been present over evolutionary timescales, but anthropogenic noise has increased rapidly in the recent past, over a timescale of a single generation for long-lived species such as the killer whale. This implies that adaptation to increased noise in these cases is ontogenetic (Rabine and Greene 2002).

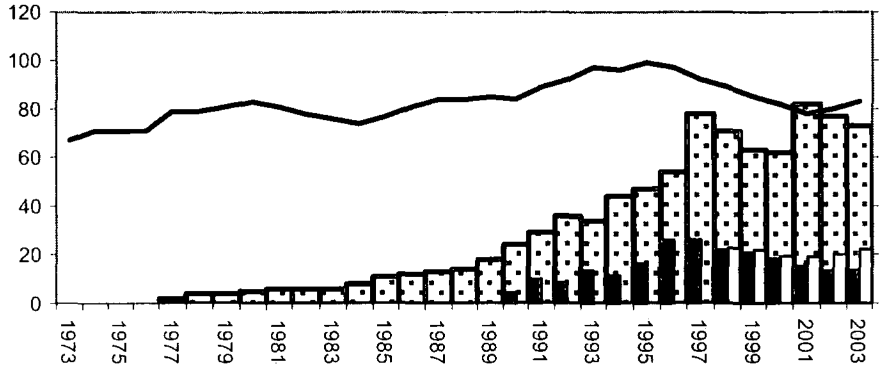
Background noise causes a reduction in the signal-to-noise ratio (Richardson et al. 1995). Increased redundancy of signals increases the receiver's performance in detection and recognition and therefore effectively increases the signal-to-noise ratio (Shannon and Weaver 1949; Wiley and Richards 1982). This can be achieved through increasing signal duration or call rate (Lengagne et al. 1999). King penguins *Aptenodytes patagonicus* have been found to increase the number of calls and the number of syllables per call under windy conditions, (Lengagne et al. 1999), Weddell seals *Leptonychotes weddelli* and harp seals *Pagophilus groenlandicus* increase call length during the breeding season to avoid masking by conspecifics (Terhune et al. 1994; Serrano and Terhune 2001), and humpback whales *Megaptera novaeangliae* lengthened their songs in response to Low Frequency Active Sonar (LFAS) playbacks (Miller et al. 2000; Fristrup et al. 2003).

Killer whales (Orcinus orca) are a cosmopolitan species, found in all of the world's oceans and have adapted to a wide range of habitats (Martin and Reeves 2002). Although there are no precise figures on the worldwide population size of killer whales, they are believed to be plentiful and not at risk as a species (Baird 2000). However killer whales have a high level of genetic differentiation between sympatric and parapatric populations and a low level of genetic variation within each population, suggesting that each population is genetically discrete and effective population size is low (Hoelzel et al. 1998, 2002). There are several well-studied populations of killer whale that have declined in numbers during the study period e.g. the Alaskan AT1 Transient, Crozet Archipelago and Southern Resident populations (Baird 1999; Osborne 1999; Matkin et al. 1999; Poncelet et al. 2002). The Southern Resident population of killer whales has been in decline since 1996 (Figure 5.1) and has recently been designated as a Threatened Population by the National Marine Fisheries Service, (NMFS) (Krahn et al. 2004), and as Endangered by the Committee on the Status of Endangered Wildlife in Canada, (COSEWIC) (Baird 1999).

This population is currently subject to intense whale-watching activity and the associated boat engine noise, with a fleet of 72 commercial vessels and an average of 22 boats following a group during daylight hours, and there has been a progressive increase in the number of boats impacting this population over the last decade (figure 5.1). Bain and Dahlheim (1994) suggested that boat noise would impair killer whale communication, as the omni-directional lower frequency component of killer whale calls is found below 10 kHz overlapping with the frequency range of boat noise. Erbe (2002) estimated that boat noise could mask calls at 1-14 km, depending on the running speed of the boat. Southern Resident killer whales appear to coordinate at least some aspects of cooperative foraging with their repertoire of discrete calls (see Hoelzel and Osborne 1986; Hoelzel 1993) and may use the different transmission properties as directionality and distance estimation cues (Miller 2002; Chapter 4).

This suggests that their ability to forage and coordinate group movement efficiently may depend on their ability to prevent acoustical masking.

Figure 5.1 Boat and whale numbers over time. Solid line indicates whale population size; grey bars indicate number of active commercial boats per year; solid bars indicate average number of boats observed following whales from shore base (Lime Kiln Lighthouse, San Juan Island, WA; data for 1990-2003 only); open bars indicate average vessel numbers following whales from boat-based observations (1998-2003 only). (courtesy of R. Osborne)



Killer whales live in matrifocal pods that show stable membership over decades (Bigg et al. 1990). Studies of the vocal repertoire of whales in the study region found pod-specific dialects (consistent with earlier studies elsewhere), and a single primary call for each pod, representing over 50% of the sounds produced by that pod (Ford 1984; Ford 1991; Hoelzel and Osborne 1986; Chapter 3). In this study I analysed the primary calls from each of the three pods that make up the Southern Resident community (Bigg et al. 1990), to test the hypothesis that vocal behaviour would change concurrent with increasing whale-watching vessel traffic, by comparing recordings with and without boat noise (in the presence or absence of boats) from three time periods: 1977-1981, 1989-1992 and 2001-2003.

Method

See chapter 2 for recording, call categorisation and analysis method and materials. I analysed the total duration (in seconds to the nearest 0.01 second using the curser function in the Canary 1.2.4 software) of the dominant call types, as at time of analysis, of each of the three Southern Resident pods J, K and L from the archive recordings; call type S1 for J pod, call type S16 for K pod and call type S19 for L pod; (figure 5.2). This was based on call usage following a year of analysis of recordings, following a further year of analysis of recordings call type S2iii became the dominant call type used by L pod, (34.8 % of total call usage), however call type S19 was still found in most L pod recordings and accounted for 26.3% of their call usage (chapter 2).

Vessel noise presence was detected aurally, and by spectral energy and waveform amplitude (figure 5.3). Recordings were categorised into those with or without motorboats present, or omitted from the study if this was ambiguous (e.g. due to other background or recording noises). Starting and stopping or changing speed were used as clear indications of the presence of motorboats. No attempt was made to quantify the number of boats present from the recordings. Call durations were compared in only two categories: motor boats present or absent for the duration of the recording.

Details of the recording and call bout lengths are provided in Table 5.1. Recordings totalled 35 hours for which the whales were near enough to provide good quality recordings and the presence or absence of boats could be clearly determined. These were chosen from over 50 hours of recordings screened. They were taken from three time periods, each roughly a decade apart; 1: 1977-1981, 2: 1989-1992 and 3:

2001-2003. All recordings used were used in their entirety, and all calls of the correct type in each recording were analysed. Recording bouts were defined as the duration between first and last call detected in a series of calls, and data were derived from a total of 89 bouts.

Figure 5.2 Spectrograms of the dominant call type of **a.** J pod, **b.** K pod and **c.** L pod and the duration parameters measured for each. (Filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752ms and 21.73 Hz)

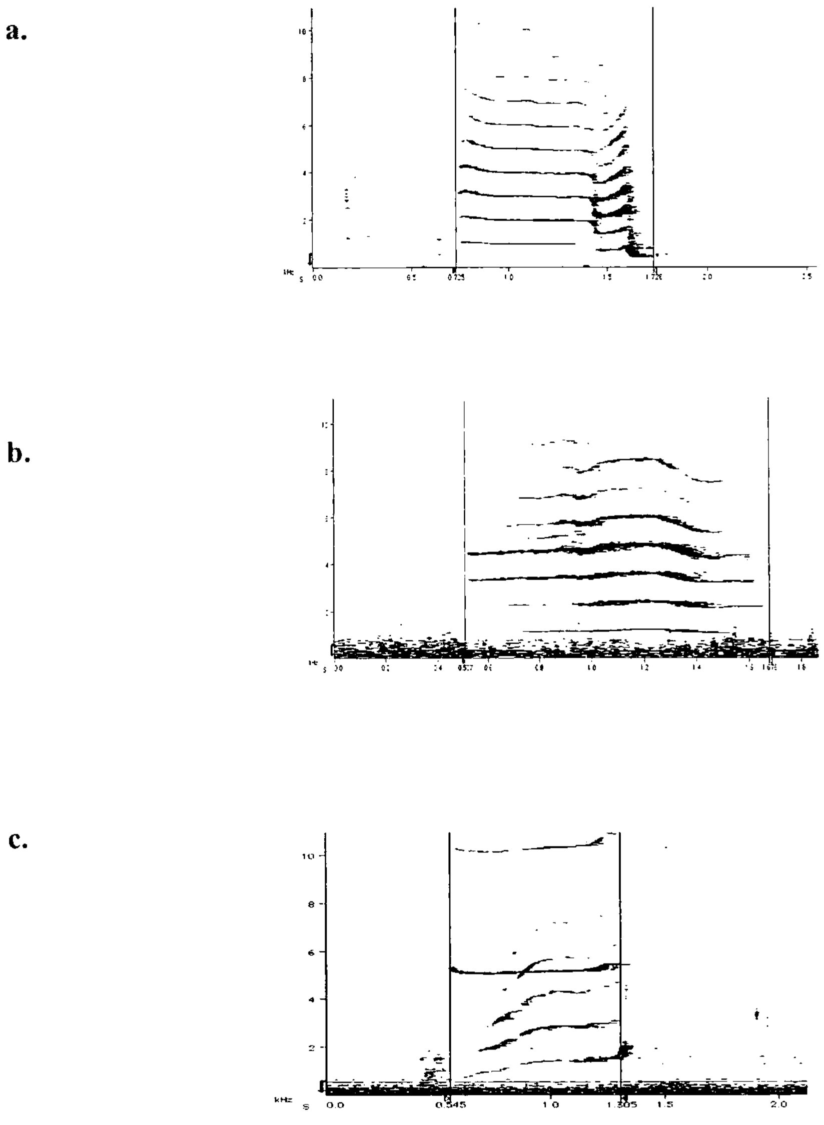
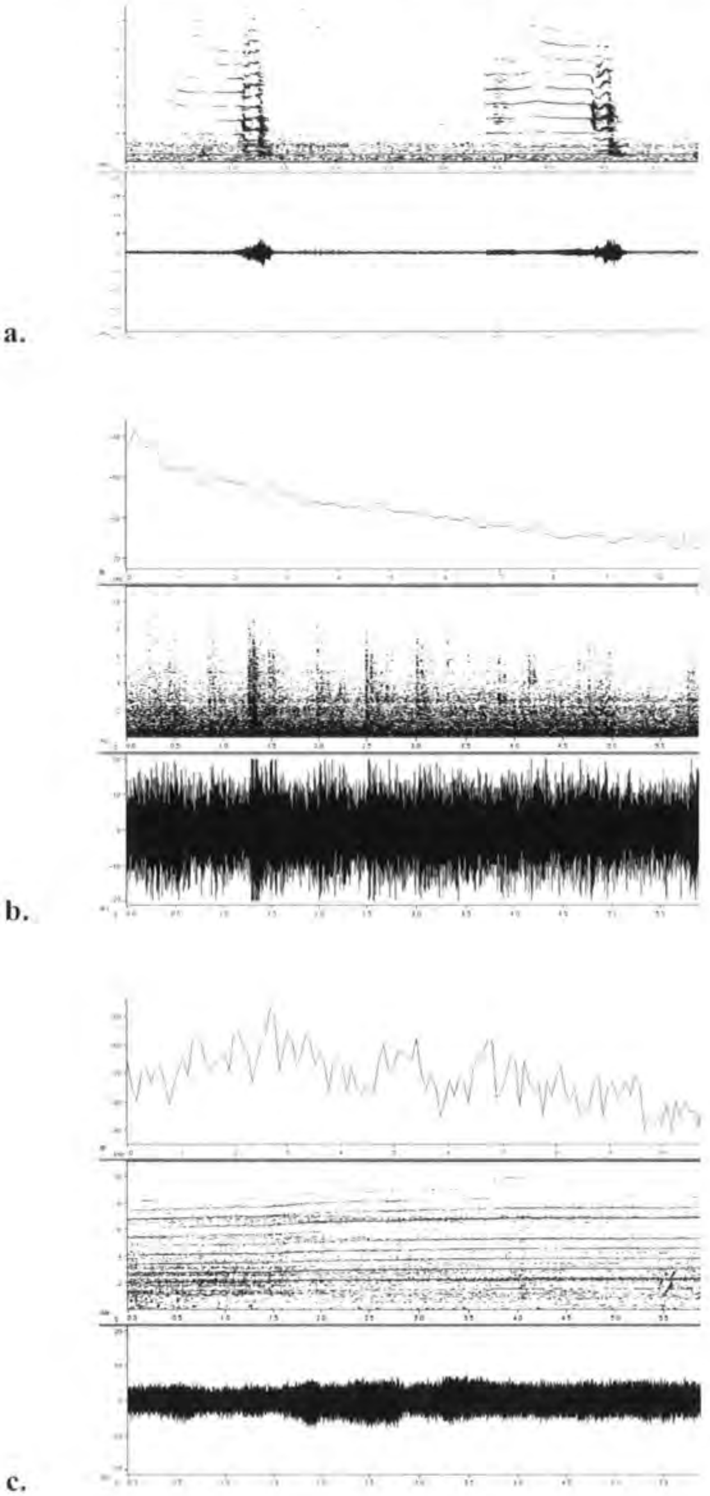


Figure 5.3a. Spectrogram and waveform of J pod in the absence of boat noise, energy spectra, spectrogram and waveform of **b.** propeller cavitation noise and **c.** outboard machinery noise all recorded in the study area. (Filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752ms and 21.73 Hz)



Counts of number of boats with whales were made by the Whale Museum, Friday Harbor from the Soundwatch Boater education program vessel for 1998-2003 and from Lime Kiln Lighthouse for 1990-2003 (see Osborne 1999).

A Kolmogorov-Smirnov test for goodness of fit was used to test for the normality of distributions (Table 5.1), and 7 of 18 tests were skewed according to this test. As non-parametric tests are conservative, both t-tests and Mann-Whitney *U* tests were used to compare all call duration distributions with and without motorboats. Call rates were compared using contingency tests. Most (80%) of the recordings without boats from the 2001-2003 time period were from an 'off peak' daytime period between 18:00 and 09:00. I therefore compared off peak against peak (09:00 – 18:00) recordings from the 1977-1981 and 1989-1992 periods (combined) to ensure that there was no underlying pattern of daytime affecting call duration.

Results

I tested the hypothesis that vocal behaviour would change concurrent with increasing whale-watching vessel traffic, by comparing recordings with and without boat noise (in the presence or absence of boats) from three time periods: 1977-1981, 1989-1992 and 2001-2003. I found no significant difference in the duration of primary calls of each pod J, K and L in the presence vs. absence of boats for the first two periods, but a significant increase in call duration for all three pods in the presence of boats during the 2001-2003 period (J-pod: $t = 4.13$, $z = 4.09$, $P < 0.0001$, d.f. = 134; K-pod: $t = 4.33$, $z = 3.36$, $P < 0.0008$, d.f. = 162; L-pod: $t = 3.14$, $z = 2.97$, $P < 0.005$, d.f. = 192; figure 5.4, table 5.1). All call-rate comparisons were non-significant.

A comparison of off peak against peak (09:00 – 18:00) recordings from the 1977-1981 and 1989-1992 periods (combined) showed no significantly greater call duration during the peak period for either t-tests or Mann-Whitney *U* tests (J-pod: $t =$

0.655, $P = 0.513$, $z = 0.336$, $P = 0.737$; K-pod: $t = 1.818$, $P = 0.071$, $z = -2.088$, $P = 0.037$; L-pod: $t = -1.198$, $P = 0.2327$, $z = -1.282$, $P = 0.1997$).

A correlation between increasing call duration over time in the absence of boats was only found for L pod (Spearman Rank Correlation Coefficient. J pod; $z = 1.315$, $P = 0.1885$, K pod; $z = 0.621$, $p = 0.5347$, L pod; $z = 4.891$, $P = 0.0001$; figure 5.5).

Years	Pod	Boat Noise	n	B	T	CR	μ	s.d.	Range	Normality	
1977-1981	J	Absent	74	19	89	3.9	0.9	0.26	0.43 - 1.82	D = 0.731	$P > 0.15$
		Present	87	20	53	4.4	0.84	0.17	0.49 - 1.17	D = 0.656	$P > 0.15$
	K	Absent	63	50	72	1.3	0.8	0.22	0.45 - 1.27	**D = 1.388**	**$P < 0.01$**
		Present	53	23	32	2.3	0.78	0.26	0.31 - 1.63	D = 0.822	$P = 0.10$
	L	Absent	42	45	132	0.9	0.62	0.14	0.29 - 0.90	**D = 1.156**	**$P < 0.01$**
		Present	44	35	181	1.3	0.67	0.1	0.46 - 0.97	**D = 0.955**	**$P = 0.04$**
1989-1992	J	Absent	96	24	33	4	0.89	0.23	0.47 - 1.50	**D = 1.209**	**$P < 0.01$**
		Present	57	13	53	4.4	0.86	0.16	0.50 - 1.28	D = 0.733	$P > 0.15$
	K	Absent	69	35	90	2	0.77	0.21	0.38 - 1.55	D = 0.772	$P > 0.15$
		Present	28	24	91	1.2	0.69	0.21	0.28 - 1.13	D = 0.622	$P > 0.15$
	L	Absent	64	36	106	1.8	0.69	0.2	0.25 - 1.20	D = 0.827	$P = 0.10$
		Present	69	24	84	2.9	0.68	0.18	0.30 - 1.09	D = 0.585	$P > 0.15$
2001-2003	J	Absent	71	27	85	2.6	0.92	0.19	0.53 - 1.31	**D = 1.895**	**$P < 0.01$**
		Present	65	12	50	5.4	1.05	0.17	0.55 - 1.47	D = 0.669	$P > 0.15$
	K	Absent	74	56	267	1.3	0.74	0.22	0.28 - 1.13	**D = 1.068**	**$P < 0.01$**
		Present	90	67	311	1.3	0.88	0.27	0.48 - 2.0	**D = 1.374**	**$P < 0.01$**
	L	Absent	135	51	204	2.6	0.75	0.18	0.36 - 1.25	D = 0.419	$P > 0.15$
		Present	59	41	162	1.4	0.84	0.2	0.49 - 1.49	D = 0.712	$P > 0.15$

Table 5.1 Details of data analyses. n = number of calls in bout; B = total duration of bouts (min); T = total duration of recording session (min); CR = call rate within call bouts (calls /min); μ = mean Call duration (sec); s.d. = standard deviation. Statistical test for normality based on Kolmogorov-Smirnov test. Significant deviations from normality are shown in bold.

Figure 5.4 Call duration (sec) for each pod comparing recordings with (black) and without (white) boats for each time period 1.(1977-81), 2.(1989-92) and 3.(2001-03) (error bars show 1 s.d.).

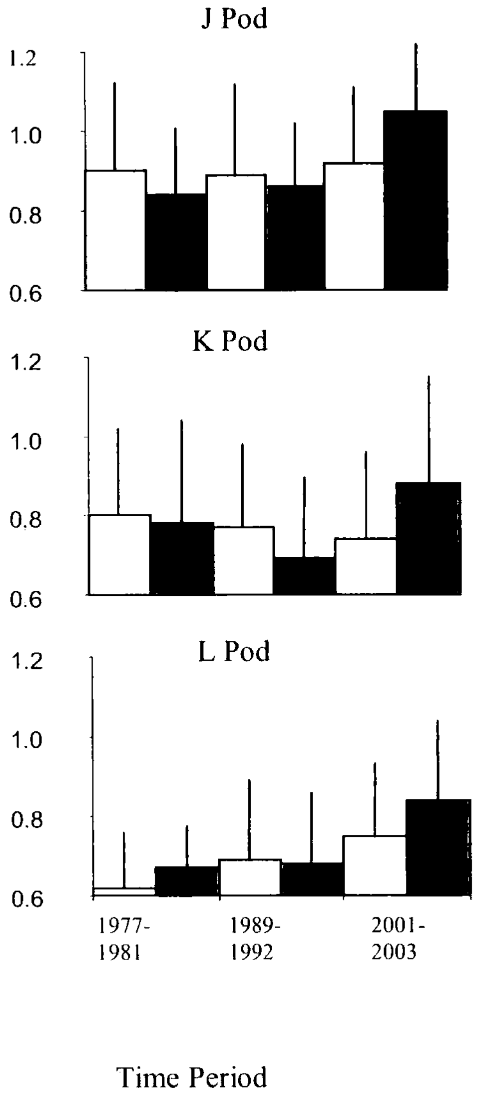
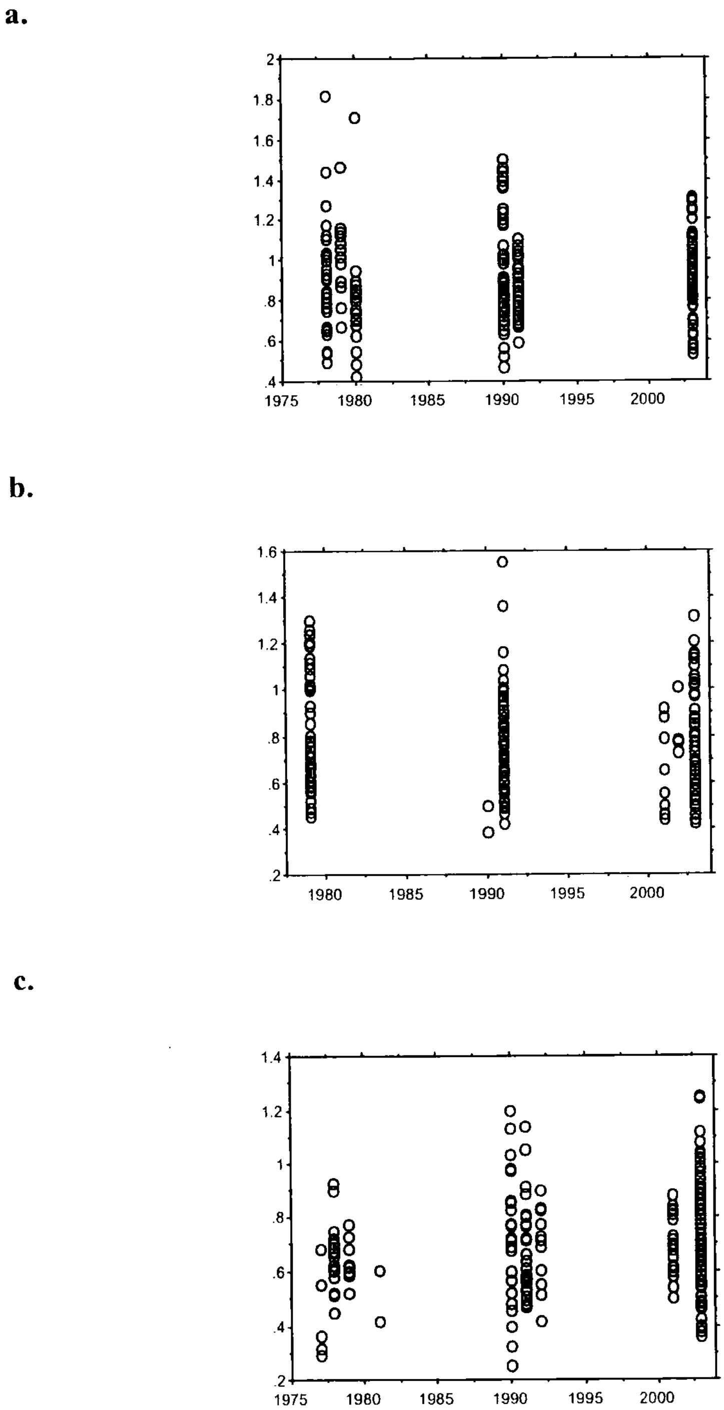


Figure 5.5 Distribution of call durations over time for **a.** J pod, **b.** K pod and **c.** L pod, from recordings with boat noise absent.



Discussion

Differences in call duration could be due to differences in behaviour, or intra-pod or individual differences (Ford 1989; Miller and Bain 2000; Nousek 2004). However as an increase in call duration in the presence of boat noise was found for all three pods following the increase in the number of tourist vessels over the past decade, it is highly suggestive that this is an anti-masking strategy. The average number of vessels attending the whales increased approximately 5-fold from 1990 to 2000, suggesting a threshold level of disturbance beyond which anti-masking behaviour began. The signal to noise ratio would have decreased as the cumulative amplitude of noise from multiple vessels increased during the 1990's, and the critical masking ratio (the signal to noise ratio at the threshold in which the signals can be detected and recognised) would have increased. Increasing the signal duration increases the redundancy and therefore the signal to noise ratio (Wiley and Richards 1982) and would therefore counteract the effect of increased noise pollution. An improved perception threshold from increased signal duration has been shown in many species (see Heil and Neubauer 2003) including odontocetes (Johnson 1967) up to a maximum duration, the time constant, beyond which there is no further increase in perception. Theoretically an increase in call duration should also correlate positively with both an increase in intra-narial pressure and source level, but this needs further investigation.

A study on the vocal behaviour of Norwegian herring feeding killer whales found an increase in the duration of the call type primarily used when feeding close to seiner vessels over the past decade, concurrent with an increase in the number of seiner vessels and whale-vessel interactions (Van Opzeeland et al. 2005).

The anti-masking strategy used should depend on the functional importance of each aspect of vocal behaviour and behavioural correlates of call rates have been found in the Southern Residents (Hoelzel and Osborne 1986), perhaps explaining why I found an effect for call duration, but not repetition rate. Noise in natural environments is rarely continuous and signallers can adapt by calling during gaps in the temporal pattern of noise (Klump 1996). Smith and Bain (2002) found that between 1999 and 2001 boats accompanied whales for up to 10 hours a day, 7 days a week and whales were not accompanied by boats in only 9% of encounters suggesting that the periods that whales are subject to continuous vessel noise may be too sustained and gaps in this noise have become too infrequent and unpredictable to use any temporal pattern of anthropogenic noise as an anti-masking strategy.

Many taxa show diurnal patterns in vocal activity e.g. birds (Klump 1996), primates (Waser and Waser 1977), humpback whales (Fristrup et al. 2003). Diurnal patterns in vocal patterns have been found in captive killer whales (Bain 1986; Ray 1986) and activity rates are lower in the Southern Residents at night (Baird et al. 2005). However I found that there was no significantly greater call duration during the peak whale watching period (09:00-18:00) than the off peak period (18:00-09:00) during the first two time periods and therefore my results are independent of any natural diurnal pattern in killer whale vocal behaviour.

Noise from vessels can be caused by the release of cavitations of bubbles between the propeller blades, which produces broadband sounds at the rate of the propeller rotation (figure 5.3b) and by machinery noise; vibrations of the moving parts transmitted through the hull to produce a continuous tones at the fundamental frequency and harmonics of the vibrations (figure 5.3c) (Urick 1983). These sounds dominate the energy spectra between 0-10 kHz (figure 5.3b and c), which coincides with the frequency range of the omni-directional lower frequency component of killer whale pulsed calls (figure 5.3a) (Hoelzel and Osborne 1986; Bain and Dahlheim

1994; Miller 2002). Masking is greatest for overlapping frequencies (Bain and Dahlheim 1994). Miller (2002) suggested that killer whales might use the relative energy detected in the omni-directional lower frequency (0-5 kHz) component and directional high frequency component (>5 kHz) due to the difference in directionality of each component, as a direction of movement cue. Masking of the lower frequency component by boat noise of an overlapping frequency range may impair this possible function of killer whale communication (Bain and Dahlheim 1994) and thus hinder pod coordination.

Theodolite studies have tracked movement patterns of killer whales and noted short-term behavioural reactions to whale watching vessels with an associated energetic cost, e.g. increased swim speeds (Kruse 1991; Williams et al. 2002) and change in travel patterns, (Jelinski et al. 2002; Smith and Bain 2002; Williams et al. 2002). The long-term effects of noise are more difficult to determine (Trites et al. 2002). Baird et al. (2005) found that the rate of deep dives had decreased between 1993 and 2002. However as their study began when there were already a high number of whale watch vessels present in this area it was not possible to determine if this was due to an increase in vessel traffic or a shift in prey abundance or behaviour (Baird et al. 2005). Morton and Symonds (2002) found that acoustic harassment devices designed to reduce harbour seal *Phoca vitulina* predation on fish farm stocks in British Columbia caused a significant reduction in sighting frequency of killer whales and concluded that the noise source had caused long-term displacement of whales from the immediate area. My results suggest a short-term response to whale watch vessel presence but one that has developed over time, between 1992 and 2001, however sightings data suggest that noise levels are not sufficient to cause displacement, as the whales' use of this area has remained stable and possibly even increased over this time period (Baird et al. 1998).

Directionality of the source of masking noise in relation to the orientation of the receiver can determine the extent of the masking effect (Richardson et al. 1995). Bain and Dahlheim (1994) found that noise from the side and behind the whale masked pure tones far less than when the noise source was directly in front of the whale. Speed, acceleration and distance of a vessel also determine the received level of boat noise and therefore the level of masking (Erbe 2002). These findings can and are being used to formulate the voluntary guidelines used by the local whale watch community to reduce masking noise.

This anti-masking strategy of lengthening call duration by the Southern Resident killer whales response to masking may or may not be a learnt one. Increasing signal duration would require relatively simple control of the respiratory system (Janik and Slater 1997, 2000; chapter 2). If the adoption of an anti-masking strategy by the Southern Residents is learnt, the timescale over which it has developed suggest it is not by vertical transmission (parent-offspring) but by horizontal transmission (across generations) or asocial learning. These processes are more able to alter behaviour to cope with rapid change in an environment than vertical transmission of behaviour or genetic evolution by natural selection (Laland 2001). Behavioural plasticity in killer whale vocal patterns and the ability to modify vocalisations through selective learning may allow them to adapt their communication system to cope with increases in background noise over ontogenetic timescales.

Structural change has been found in the acoustic signals of great tits *Parus major* in a human-altered environment (Slabbekoorn and Peet 2003), and rapid change in acoustic signal may be assisted by a vocal learning abilities in many bird species. Comparatively few mammals are vocal learners (Janik and Slater 1997) and this may explain why killer whales are one of very few mammal species, for which change in acoustic behaviour due to anthropogenic noise has been described. However it is not known if killer whales have the capacity to fully compensate for masking by boat noise or the energetic cost of increased signal output.

Chapter 6 - Ecological correlates of call type fundamental frequency.

Introduction

Acoustic communication is often constrained by ambient, biological and anthropogenic background noise or the risk of alerting unwanted eavesdroppers such as predators, prey or competitors (Au et al. 1985; Barrett-Lennard et al. 1996; Lengagne et al. 1999; Grinnell and McComb 2001; Slabbekoorn 2004; Foote et al. 2004; Deecke et al. 2005; chapter 5).

These obstacles to effective communication can often be overcome by adjusting the frequency range of a signal so that it does not overlap with the sound source or the hearing range of eavesdroppers, (e.g. Au et al. 1985; Rydell and Arlettaz 1994). This can lead to divergence in signal structure between individuals or populations of the same species e.g. urban populations of great tits *Parus major* have been found to sing at a higher frequency than rural populations lessening masking by traffic noise (Slabbekoorn and Peet 2003).

In some species a change in signal frequency range has been used to exploit new resources, e.g. Kingston and Rossiter (2004) found that three distinctive morphs of the long-eared horseshoe bat *Rhinolophus philippinensis* each had a distinctive frequency range of echolocation signal to exploit a different range of prey species. As echolocation in this species also has a communication and assortative mating function, acoustic divergence has led to genetic, physiological and morphological divergence between the sympatric morphs (Kingston and Rossiter 2004).

Three sympatric ecotypes of killer whale have been found in the North-eastern Pacific, two are predominantly found in nearshore waters, (resident and transient types) and one is found most commonly 15 km or more offshore but is occasionally sighted in the nearshore water (offshore type; Ford et al. 2000, Krahn et al. 2004).

Behavioural observations and analysis of stomach contents have revealed that the two nearshore eco-types are dietary specialists (Baird and Dill 1995; Ford et al. 1998; Saulitis et al. 2000; Heise et al. 2003; Herman et al. 2005). Resident killer whales are piscivorous and thought to favour salmonids, transient killer whales specialise in foraging for marine mammals (Baird and Dill 1995; Ford et al. 1998; Saulitis et al. 2000; Heise et al. 2003; Herman et al. in 2005). Comparatively little is known about the diet of offshore killer whales. It is thought they are also mainly piscivorous (Ford et al. 2000; Black et al. 2002; Herman et al. 2005). Fatty acid and stable isotope analyses suggest they are feeding at a high trophic level (Herman et al. 2005) and indirect evidence such as their ragged fins and worn down teeth suggests that they may specialise in hunting elasmobranches (D. Bain Personal communication). The three eco-types are genetically highly differentiated at both mitochondrial and nuclear loci (Hoelzel and Dover 1991; Hoelzel et al. 1998, 2002; Barrett-Lennard 2000) but have not yet been designated as separate species as it is not possible to determine whether this differentiation arises from low levels of ongoing migration or a recent cessation of migration (Hoelzel et al. 2002; Waples and Clapham 2004).

Resident and offshore ecotypes vocalise at high call rates across a range of contexts (Hoelzel and Osborne 1986; Ford et al. 2000; Deecke et al. 2005) including foraging (Hoelzel and Osborne 1986). Vocal communication in transients is constrained by the excellent hearing abilities of their marine mammal prey whose hearing range overlaps with the frequency range of the calls of killer whales (figure 6.1; Deecke et al. 2005). Strong behavioural responses to killer whale call playbacks have been found in belugas *Delphinapterus leucas* (Fish and Vania 1971), Steller's sea lions *Eumetopias jubatus* (Akamatsu et al. 1996) and harbour seals *Phoca vitulina* (Deecke et al. 2002). Transients call rates are significantly lower than residents

(Deecke et al. 2005) and they call during fewer contexts. Transient calling occurs predominantly during social behaviour, which occurs much less frequently than in residents, or following a kill (Ford 1984; Morton 1990; Deecke et al. 2005; Saulitis et al. 2005). Transients also produce much shorter echolocation click trains than residents and the inter-click interval is less regular and therefore more cryptic and difficult to detect than residents (Barrett-Lennard et al. 1996).

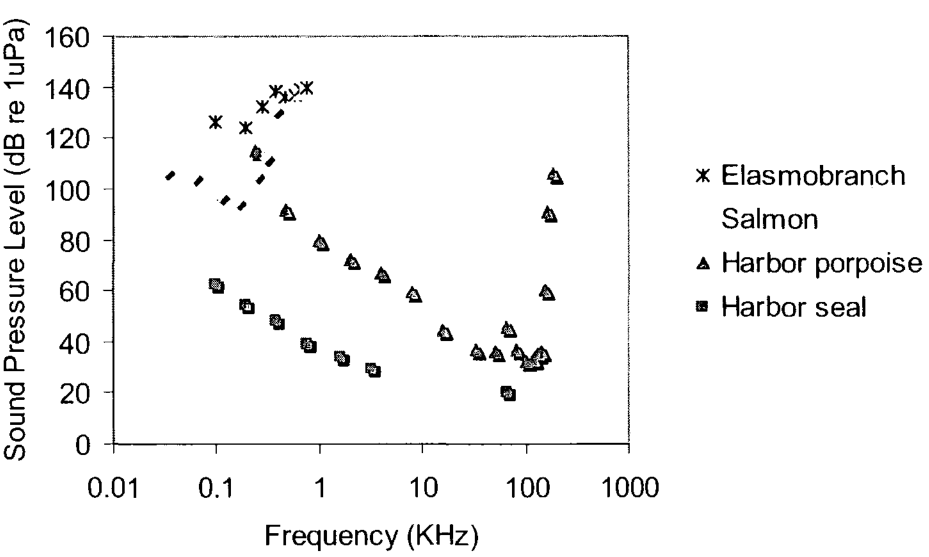


Figure 6.1 Audiograms of the little skate *Raja erinacea* (Casper et al. 2003), Atlantic salmon Salmo salar (Hawkins and Johnstone 1978), harbour porpoise *Phocoena phocoena* (Kastelein et al. 2002), and harbour seal *Phoca vitulina* (Kastak and Schusterman 1998).

Ecology could also affect call structure as well as call usage. Salmonid and elasmobranch species have narrowband low frequency hearing ranges (Hawkins and Johnstone 1978; Myrberg 2001; figure 6.1), small marine mammals have a broadband hearing range but are more sensitive to higher frequencies (Kastak and Schusterman 1998; Kastelein et al. 2002; figure 6.1). Ambient noise has a peak spectral energy below 1 kHz (Urick 1983) and can lower the signal to noise ratio and reduce the range of a signal (Richardson et al. 1995) and may be higher in offshore waters (Urick 1983), though anthropogenic effects will be important in this context.

In this chapter I compare the minimum and maximum fundamental frequency of call types of each of the three ecotypes to assess if their different ecological niches have led to differences in call structure.

Methods

Recordings were made on equipment with a flat response between 0.10 and 10 kHz. Digitisation and call categorisation were carried out using the same methodology as chapter 2.

I analysed 89 minutes from three recording sessions of Offshore killer whales from 2004 and identified and categorised 187 calls into 7 call types (see appendix ii), I compared the entire known repertoires of five well-studied populations and the call types categorised from the offshore recordings, complementing my data with published data in some cases. I measured the mean maximum and minimum frequency of the fundamental of one example of each call type from the Southern Resident repertoire and from my Offshore recordings. As call types are highly stereotyped and there is low CV of frequency parameters (Ford 1987; Miller and Bain 2000; Saulitis 1993) the examples selected should therefore be representative of that call type. Additionally the mean frequency parameters measured for that Southern Resident call type in Hoelzel and Osborne (1986) and Ford (1987) were used as a reference to make sure that the frequency parameters of my examples fell within the normal range for that call type. Using the measurement panel in Canary 1.2.4 software I was able to measure frequency parameters to a resolution of 0.01 kHz. I then supplemented these with data from the literature using measurements from Ford (1987) for the Northern Residents and West Coast Transients, from Filatova et al. (2004) for the Kamchatka Residents and from Saulitis et al. (2005) for the AT1 Transients. Where the minimum or maximum frequency was not given a micrometer was used to measure from the published spectrogram. For two-component call types I only measured the low frequency component. If there were two or more subtypes of a call type, e.g. N32i and N32ii, I used the measurement of the subtype with the lowest minimum frequency and the highest maximum frequency, so that a single pair of measurements represented all the subtypes of a particular call type. Measurements were taken or rounded to the nearest 0.1 kHz. I compared the mean maximum and minimum call type fundamental frequencies between populations using a non-parametric Mann Whitney U-test.

Results

Although the techniques used in some measurements were coarse, I found homogeneity in the mean and range of maximum fundamental frequency of call types within the repertoire when comparing between populations of the same ecotype (table 6.2, figure 6.2). I also found homogeneity in the mean and range of minimum fundamental frequency of call types within the repertoire when comparing between resident populations, but not between the two transient populations.

All three resident populations had call types in their repertoires with a maximum fundamental frequency over 3 kHz higher than the maximum fundamental frequency of any call types in either of the two transient population's repertoires. However there were no consistent differences in the mean minimum or mean maximum fundamental frequency between resident and transient call type repertoires.

Offshores had both a significantly higher mean maximum and minimum call type fundamental frequency than all the other populations (table 6.2, figure 6.3).

a.	Number of call types	Mean (kHz)	S.D.	Range (kHz)
AT1 Transients	10	0.6	0.3	0.5-1.3
West Coast Transients	8	0.3	0.1	0.1-0.4
Southern Residents	28	0.5	0.3	0.1-1.2
Northern Residents	43	0.4	0.3	0.1-1.2
Kamchatka Residents	19	0.5	0.2	0.1-0.8
Offshores	7	0.9	0.3	0.6-1.6
b.	**Number of call types**	**Mean (kHz)**	**S.D.**	**Range (kHz)**
AT1 Transients	10	0.9	0.5	0.5-2.0
West Coast Transients	8	1.3	0.8	0.2-2.6
Southern Residents	28	1.6	1.3	0.2-6.4
Northern Residents	43	2	1.5	0.4-6.6
Kamchatka Residents	19	2.1	1.4	0.7-6.0
Offshores	7	3.5	1.9	1.4-5.4

Table 6.1a. Minimum and **b.** maximum fundamental frequencies of call types in the repertoires of six Pacific killer whale populations.

Discussion

Differences in whistle structure have been found between neighbouring bottlenose dolphin communities and appear to result from learning occurring between individuals from within the same community and then random drift between neighbouring communities rather than ecological differences (Fripp et al. 2005). Killer whale call structure changes over time in a non-directional manner due to cultural drift and these changes are copied between closely associating groups from within the population (Deecke et al. 2000). If the ecotypes had diverged only once an evolutionary significantly amount of time prior to a further split into the different

Table 6.2. Comparison of **a.** the mean minimum and **b.** the mean maximum fundamental frequencies between six Pacific killer whale populations. Shaded results indicate a significant difference between populations.

a.

West Coast Transients	$z = 3.55$, $p < 0.001$				
Southern Residents	$z = 1.18$, $p = 0.24$	$z = 2.055$, $p = 0.040$			
Northern Residents	$z = 1.98$, $p = 0.048$	$z = 0.142$, $p = 0.89$	$z = 1.87$, $p = 0.06$		
Kamchatka Residents	$z = 1.35$, $p = 0.18$	$z = 1.89$, $p = 0.059$	$z = 0.44$, $p = 0.66$	$z = 1.50$, $p = 0.13$	
Offshores	$z = 2.29$, $p = 0.022$	$z = 3.24$, $p = 0.0012$	$z = 2.50$, $p = 0.012$	$z = 3.12$, $p = 0.0018$	$z = 3.18$, $p = 0.0015$
	AT1 Transients	**West Coast Transients**	**Southern Residents**	**Northern Residents**	**Kamchatka Residents**

b.

West Coast Transients	$z = 1.24$, $p = 0.21$				
Southern Residents	$z = 2.22$, $p = 0.026$	$z = 0.61$, $p = 0.54$			
Northern Residents	$z = 3.035$, $p = 0.0024$	$z = 1.68$, $p = 0.092$	$z = 1.46$, $p = 0.14$		
Kamchatka Residents	$z = 3.074$, $p = 0.0021$	$z = 2.018$, $p = 0.044$	$z = 1.88$, $p = 0.061$	$z = 0.28$, $p = 0.78$	
Offshores	$z = 2.88$, $p = 0.004$	$z = 2.55$, $p = 0.011$	$z = 2.54$, $p = 0.011$	$z = 1.93$, $p = 0.0054$	$z = 1.97$, $p = 0.049$
	AT1 Transients	**West Coast Transients**	**Southern Residents**	**Northern Residents**	**Kamchatka Residents**

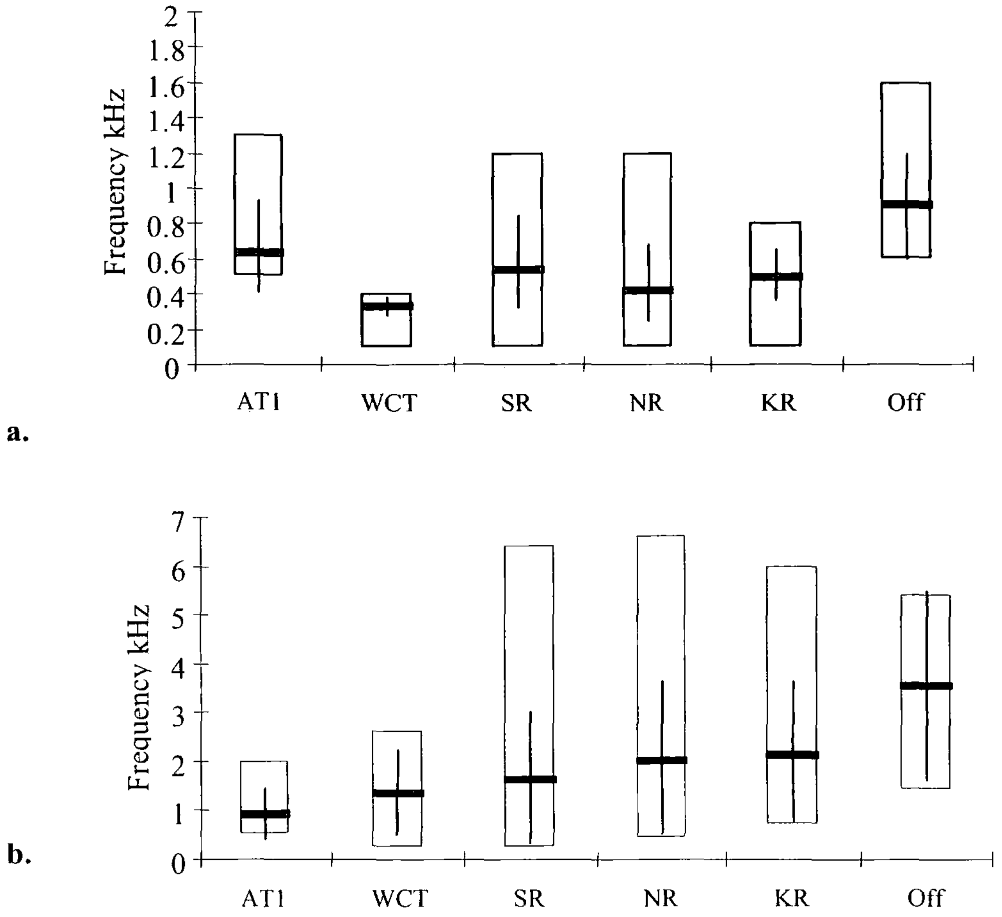


Figure 6.2 The distribution of **a.** minimum and **b.** maximum fundamental frequency of call types in the repertoires of six Pacific killer whale populations. Dark lines are means, boxes represent the range and whiskers indicate standard deviation.

populations of the same ecotype, then drift could explain the observed differences between ecotypes and the relative homogeneity between populations of the same ecotype. However many of the call types with similar fundamental frequencies had very different frequency contour modulations and although the AT1 transients produce one call type (call 3) that is similar to a West Coast transient call type (T1), the others are distinctively unique to that population (Saulitis et al. 2005), as are most call types within the repertoires of each resident population (Ford 1991). Additionally a comparison with populations from other ocean basins suggests that directional ecological selection on the fundamental frequency range of killer whale call types is responsible. Fundamental frequency range of call types produced by Atlantic nearshore fish-eating Norwegian killer whales (Moore et al. 1988) are comparable with those found for the Pacific resident populations. Awbrey et al. (1982) found the calls recorded from killer whales in offshore Antarctic waters were higher in frequency than North-eastern Pacific resident calls similar to those produced by Pacific offshore killer whales.

The differences in ecology of each ecotype are likely to have been present over evolutionary timescales and so this directional change could have been by the relatively slow process of natural selection. However the plasticity of killer whale vocal behaviour (chapters 2 & 5) would allow the shaping of killer whale call structure by ecology to take place rapidly after a founding event of a foraging tradition. This could then be followed by slow non-directional structural change due to drift (e.g. Deecke et al. 2000), but within the boundaries determined by the ecological niche.

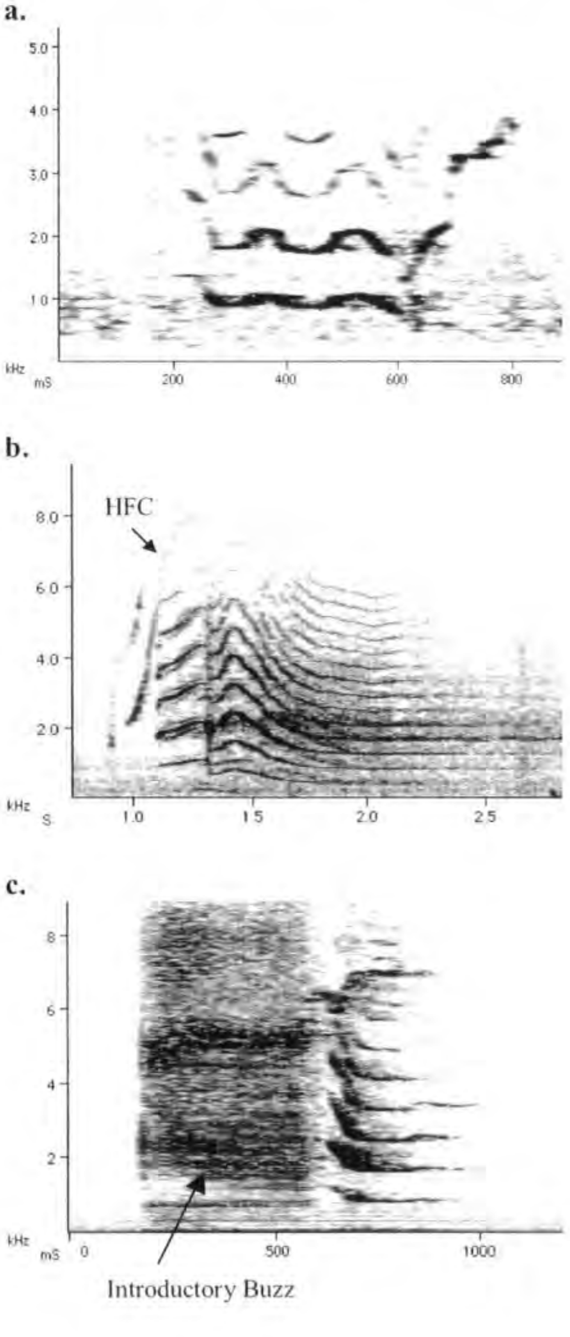
Differences in ambient noise spectral profiles could have caused this divergence in signal structure. Offshore killer whales spend more time than either of the nearshore ecotypes in an acoustic environment with higher expected levels of background noise from ambient noise sources such as wind and wave noise. Underwater ambient noise is broadband in character and above 500 Hz it is dominated by wind and wave generated noise (Urick 1983) and the level of noise is most closely correlated with wind speed (Wille and Geyer 1984) increasing 5 dB with each doubling of wind speed from 2.5 to 40 knots (Wenz 1962). Between 500 Hz and 5 kHz spectrum level decreases 5 dB per octave with increasing frequency (Wenz 1962). Surf noise is a major component of nearshore waters but this would be reduced in the sheltered fjord-like waterways of the North-eastern Pacific and sound propagation would also be less in waterways with twists and turns compared to the open sea (Urick 1983). Therefore the lower frequency section of the ambient noise spectrum levels above 500 Hz is likely to be much higher for offshores than either of the nearshore ecotypes.

Selection of an 'acoustical niche' outside the frequency band of masking source has been noted in several species (e.g. red-winged blackbirds *Agelaius phoeniceus* Brenowitz et al. 1982; beluga *Delphinapterus leucas* Au et al. 1995; great tits *Parus major* Slabbekoorn and Peet 2003; pygmy marmosets *Cebuella pygmaea* De la Torre and Snowdon 2002). Mossbridge et al. (1999) previously found that a population of Antarctic killer whales adjusted the frequency range of modulations of their whistles during December, when sympatric leopard seals *Hydrurga leptonyx* are vocal, to a frequency range outside the frequency range of leopard seal calls.

Although there were no consistent differences in the mean fundamental frequency between resident and transient call type repertoires (table 6.2, figure 6.2) each fish-eating resident population's repertoires contained call types with a maximum fundamental frequency 3 kHz higher than found in either marine mammal eating transient population's call type repertoires (figure 6.2b). However these differences do not appear to result from calls occupying an 'acoustic niche' outside the hearing range of prey species. Some resident call types have fundamental frequencies below 500 Hz (figure 6.3) and some call types start off with an introductory broadband buzz, which contains energy below 500 Hz, suggesting that salmon would be able to detect these (Hawkins and Johnstone 1978; figure 6.3). Simon (2004) recently found a call type that was used by Icelandic killer whales almost exclusively in conjunction with tail slaps during carousel feeding on Herring

Clupea harengus. This call has a fundamental frequency that overlaps with the herring's peak hearing and which may aid the whale

Figure 6.3 Examples of **a.** an offshore call type, **b.** a transient call type and **c.** a resident call type. (Filter bandwidth of 88.24, FFT size 1024 and 87.5% overlap, resulting in a grid resolution of 5.752 ms and 21.73 Hz).



in herding schools together before they debilitate them with a tail slap (Simon 2004). It may be that residents also use call types with a lower fundamental frequency that overlap with the hearing range of salmon to manipulate their behaviour. Janik (2000b) was able to determine that bottlenose dolphins *Tursiops truncatus* in the Moray Firth used low frequency bray sounds when pursuing salmonid prey and suggested such a role for this vocalisation. Localisation of individual whales using multi-hydrophones and concurrent behavioural observations are needed to determine if resident killer whales may use sounds to debilitate their prey.

The fundamental frequency is not necessarily indicative of the spectral profile of the frequency content of killer whale calls. Transient call types may have a low mean fundamental frequency but they contain a broadband range of harmonics ranging to over 40 kHz (Miller 2002). Some transient call types also contain an overlapping tonal high frequency component (Ford 1987; Deecke 2003; Saulitis et al. 2005 figure 6.3) that has harmonics ranging to over 100 kHz (Bain and Dahlheim 1994) overlapping with the peak hearing range of the harbour seals and harbour porpoise (Kastak and Schusterman 1998; Kastelein et al. 2002; figure 6.1, 6.3). Therefore a killer whale call type with a low fundamental frequency should be as detectable by harbour seals and harbour porpoises within the active space of the call as those with a high fundamental frequency. A possible exception may be the AT1 transient call 6 (Saulitis et al. 2005) which has a low fundamental frequency always below 900Hz and of which the harmonics are rarely observable in the spectrogram. This may explain why the AT1 transients are able to use this call type during foraging (Saulitis et al. 2005), while other transients remain silent during foraging (Deecke et al. 2005).

A number of species predictably produce signals of different frequencies in different contexts (Marler 1967, 1977). For example the call types that are frequently used during resting behaviour by different clans within the Northern Residents have a low maximum fundamental frequency (Ford 1989). Residents call across a range of contexts, whereas transients normally only vocalise following a successful kill or during surface active behaviour (Deecke et al. 2005; Saulitis et al. 2005) The difference in fundamental frequency range between ecotype may reflect differences in the range of contexts across which they normally vocalise.

There is an apparent positive correlation between source level and pulse repetition rate, and consequently fundamental frequency, in production of pulsed sounds by odontocetes (Cranford et al. 2000) including killer whales (Miller 2000). The range of source levels for the Southern Resident call types (range of 137 to 157, mean of 145 dB *re* 1 µPa@1 m, Veirs 2004) is almost identical to that found for the range of source levels for the Northern Resident call types (range of 138 to 156, mean of 146 dB *re* 1 µPa@1 m Miller 2000). If the fundamental frequency is an accurate indicator of source level, my results may reflect the similar range of distances over which calls are used to maintain contact between individuals and groups. Transient calls are often faint in comparison to resident calls (Deecke et al. 2005). The constraints placed on transient killer whale's vocal behaviour by its acoustically sensitive prey (Deecke et al. 2002, 2005) may have selected for calls with a lower active space to minimize the area in which prey is alerted to their presence. Again, if the fundamental frequency does indicate the source level, this may explain why transients do not produce call types to such a high fundamental frequency as some resident call types. However source pressure level measurements and estimates of active space of transient calls are necessary to test this hypothesis.

Geographic variation in vocalisation structure due to ecological differences has been found in many species, however my results are unusual in that killer whale eco-types are sympatric. Some sympatric bat, bird and insect species have undergone parallel changes in signal structure and fitness traits due to ecological selection (Wells and Henry 1998; Slabbekoorn and Smith 2002; Kingston and Rossiter 2004). Signal structure could then provide acoustic cues for females to find males adapted to a particular niche leading to sympatric ecological speciation (Wells and Henry 1998; Slabbekoorn and Smith 2002; Kingston and Rossiter 2004). Killer whale ecotypes have undergone phenotypic divergence and the physiological differences between the ecotypes are mirrored in each of the sympatric resident and transient populations in the Pacific Northwest (Matkin et al. 1999; Ford and Ellis 1999; Ford et al. 2000) suggesting directional change. If these phenotypic traits are advantageous to one ecotype but a disadvantage to another (e.g. Fung and Barrett-Lennard 2004), then it may be beneficial for females to use acoustic cues determined by ecology to select males with a similar foraging tradition. This may have helped to maintain genetic differentiation following separate founding events that we see between eco-types of killer whale in the Pacific Northwest, despite a lack of external barriers to gene flow (Hoelzel and Dover 1991; Hoelzel et al. 1998, 2002; Barrett-Lennard 2000).

Chapter 7 – Conclusions.

Synthesis

Recent research into the evolution of killer whale stereotyped call type usage and call structure has concluded that the changes they detected were the result of directionless change due to drift (Ford 1991; Deecke et al. 2000; Miller and Bain 2000; but see Yurk et al. 2002). However in this thesis I have also shown that under certain contexts directional change can occur or seem the most likely explanation for patterns of variation detected. Directional change could occur due to some form of pressure e.g. anthropogenic noise, ambient noise, social structure, etc. Each pressure may impact acoustic communication over a different timescale. The pressures caused by the ecology of each ecotype such as the hearing abilities of their preferred prey or the ambient noise levels in the habitat of their home range would have been present over evolutionary timescales and may be significant enough to have led calls to evolve slowly by natural selection. Some change due to social structure may also be a slow process e.g. the gradual fission of a pod can take many years, however it can happen in the lifetime of a single individual (see chapter 2). Likewise the recent, rapid increase in anthropogenic noise in the world's oceans requires a rapid rate of adaptation to avoid masking of communication. The behavioural plasticity allowed by a vocal learning ability means that killer whales could change their acoustic behaviour rapidly when under selective pressure to do so. However there also appears to be conformism and slow change of killer whale stereotyped call type usage. Kin recognition in a species for which kin-directed behaviours such as allo-parenting and food provisioning have been noted, seems the most probable pressure on conservative change and conformist transmission of vocal repertoires. The correlations of call usage presented here suggest a multi-layered recognition system. Intra-pod call types are almost exclusive to that pod and inter-pod shared call types used to signal affiliation between commonly associating pods. This communication system can adapt rapidly through change to both call structure and call use in response to social or ecological change.

Future Research

In chapter 4 and 6 I found behavioural correlations that suggest the production and usage of call types may depend upon their transmission properties, which may in turn be dependent upon the sound production mechanisms. Based on investigations on bottlenose dolphins, pulsed and tonal sounds in odontocetes are both produced by air pressure being built up below the bony nares and expelled through the phonic lips (Cranford 2000), tonal sound production correlates positively with intra-narial pressure and source level (Cranford 2000), possibly explaining why calls that contain an overlapping tonal HFC have a higher source pressure level than those without. If the pulsed component is the result of vibrations in air in the nasal sacs then it will suffer from an impedance mismatch between air and tissue and internal reflection reducing directionality and intensity (Cranford 2000). The tissue borne HFC will be impedance matched to the aquatic environment (Cranford 2000), making it more intense at source than the LFC as found by Bain and Dahlheim (1994). Focusing the energy of a sound into a narrowband, directional beam also increases its transmission properties if the receiver is on axis (Wiley and Richards 1982; Brown 1982). Finally the frequency range of the harmonics of the HFC overlap with the killer whales' most sensitive hearing range, 18-42 KHz (Szymanski et al 1999), further increasing the active space of these call types (Miller 2000). However this requires further experimental investigation specifically on killer whales to fully understand the production of two-component call types. Additionally recordings using acoustic tags with a time depth recorder or a multi-hydrophone array capable of localising in three dimensions could be used to compare vocalisations at different depths. If the resonance medium is air it would cause a change with depth, but if a call component resonates in dense tissue then it should be less prone to changes with depth.

Multi-hydrophone arrays capable of localising individuals could be used to address many questions, such as by recording identified individuals in multi-pod groups to see in inter-pod call type matching is occurring or during a direction change to see if two-component call types are used by individuals who start this change.

Further investigation is needed on the impact of anthropogenic noise on the killer whales. Modern acoustic tags which incorporate time, depth, motion and heat flux recorders would give us accurate received levels and allow investigation of energetic, physical and vocal behavioural response to a range of received levels. Additionally source level measurements of the range of vessel types and at a range of speeds and distances are necessary to produce objective meaningful whale watching regulations.

Summary

I have added to the already strong evidence for a vocal learning ability in killer whales and shown how infant killer whales depend upon both production and usage learning to develop the call type repertoires found in adult killer whales. The pod-specific repertoires appear to be stable over decadal timescales under a normal social context. The proportional call usage of each pod also depends upon social structure and less cohesive pods use a higher proportion of two-component call types, which have a higher active space. These call types are also used in inter-pod interactions. The Southern Resident population of killer whales have adopted a strategy over the past decade of increasing call type duration in the presence of boat noise to avoid masking by whale watching boats, which have increased in number concurrently. There are also differences in the range of call type fundamental frequency within the repertoires of populations of different ecotypes and I suggest that differences in the level of ambient noise and the range of contexts in which calls were used could be responsible.

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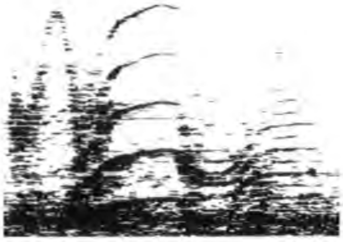
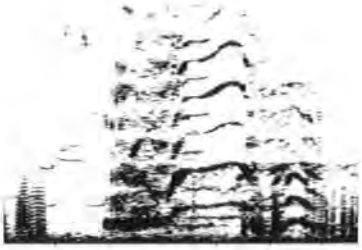
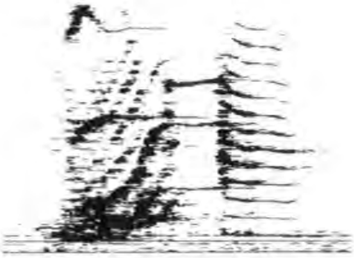
Appendix i. An index of spectrograms of call types produced by the Southern Resident killer whale population, using the alphanumeric system of Ford 1987.


S1


S2i


S2ii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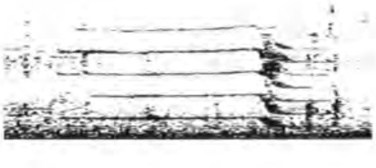
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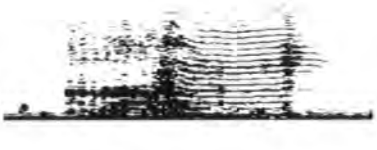
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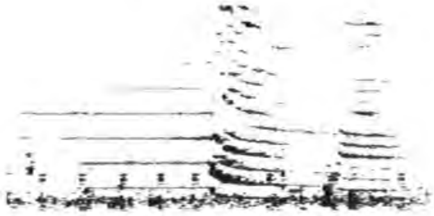
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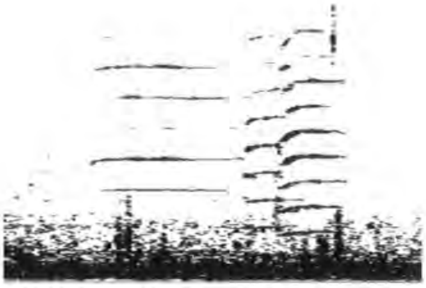
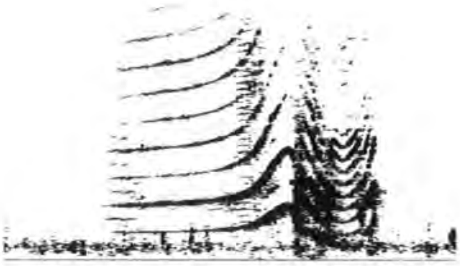
S8



S9

S10



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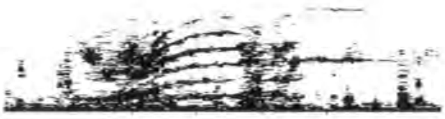
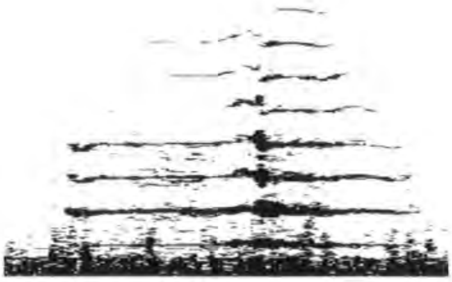
S13

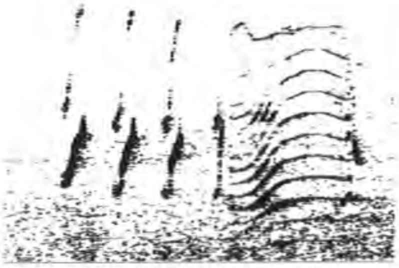


S14

S16



S17


S18


S19


S22


S31


S33

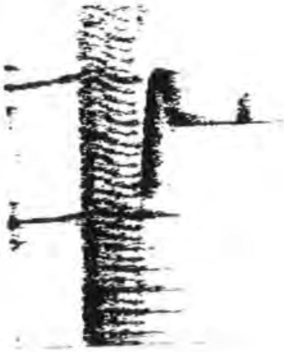

S36


S37i


S37ii

S40

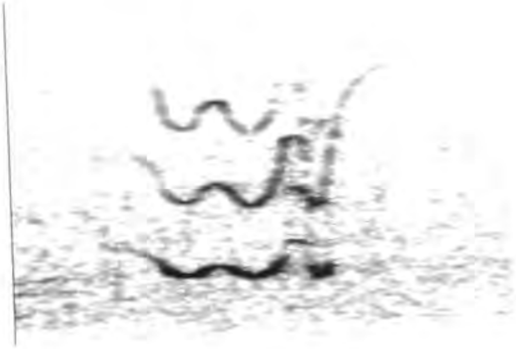
S41

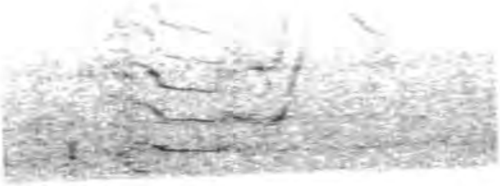


S42

S44

Appendix ii Call types identified from my recordings of the Offshore killer whale population.
nb. This based on a limited sample size (see chapter 6 for details) and is meant to accompany chapter 6 and not be an exhaustive catalogue of the Offshore killer whale population.





Appendix iii. A list of recording sessions analysed for this thesis.

Date	Start Time	Pods	Source
18-Aug-77	20:15	J, K	K. C. Balcomb, The Center for Whale Research
11-Sep-77	19:59	L	K. C. Balcomb, The Center for Whale Research
10-Oct-77	14:45	J	K. C. Balcomb, The Center for Whale Research
10-Oct-77	14:53	J	R. Osborne, The Whale Museum
16-Oct-77	17:13	J	R. Osborne, The Whale Museum
16-Oct-77	17:35	J	R. Osborne, The Whale Museum
11-Feb-78	16:11	J	K. C. Balcomb, The Center for Whale Research
31-Jul-78	14:55	J	R. Osborne, The Whale Museum
8-Aug-78		J, K, L	K. C. Balcomb, The Center for Whale Research
17-Aug-78		J, K, L	K. C. Balcomb, The Center for Whale Research
26-Aug-78		J, K, L	K. C. Balcomb, The Center for Whale Research
26-Aug-78	16:35	J, K, L	R. Osborne, The Whale Museum
12-Sep-78	15:14	L	R. Osborne, The Whale Museum
12-Sep-78	15:14	L	K. C. Balcomb, The Center for Whale Research
12-Sep-78	17:03	L	K. C. Balcomb, The Center for Whale Research
12-Sep-78	16:31	L	R. Osborne, The Whale Museum
23-Sep-78	2:45	J, K, L	R. Osborne, The Whale Museum
23-Sep-78	13:33	L	R. Osborne, The Whale Museum
23-Sep-78	15:13	L	R. Osborne, The Whale Museum
25-Sep-78	10:41	J, K, L	R. Osborne, The Whale Museum
28-Sep-78	18:14	J, K, L	R. Osborne, The Whale Museum
13-Oct-78	15:20	L	R. Osborne, The Whale Museum
20-Oct-78	22:15	L	K. C. Balcomb, The Center for Whale Research
24-Nov-78	13:50	J, K	K. C. Balcomb, The Center for Whale Research
13-Jun-79	15:00	J	R. Osborne, The Whale Museum
16-Jun-79	14:31	J	K. C. Balcomb, The Center for Whale Research
17-Jun-79	9:38	J	K. C. Balcomb, The Center for Whale Research
18-Jun-79	18:18	J	K. C. Balcomb, The Center for Whale Research
24-Jun-79	10:40	J, K, L	K. C. Balcomb, The Center for Whale Research
30-Jun-79	17:45	J, K	K. C. Balcomb, The Center for Whale Research
3-Jul-79	6:15	J, K	K. C. Balcomb, The Center for Whale Research
5-Jul-79	15:10	J, K	K. C. Balcomb, The Center for Whale Research
10-Jul-79		J, K, L	K. C. Balcomb, The Center for Whale Research
5-Aug-79		K	K. C. Balcomb, The Center for Whale Research
8-Aug-79	23:46	J, K	K. C. Balcomb, The Center for Whale Research
10-Aug-79	21:45	J	K. C. Balcomb, The Center for Whale Research
11-Aug-79	7:50	J	K. C. Balcomb, The Center for Whale Research
11-Aug-79	10:58	K	K. C. Balcomb, The Center for Whale Research
13-Aug-79	8:27	K	K. C. Balcomb, The Center for Whale Research
13-Aug-79	9:05	K	K. C. Balcomb, The Center for Whale Research
16-Aug-79	18:32	J	K. C. Balcomb, The Center for Whale Research

17-Aug-79		J	K. C. Balcomb, The Center for Whale Research
1-Sep-79		J	K. C. Balcomb, The Center for Whale Research
13-Sep-79		J, K, L	K. C. Balcomb, The Center for Whale Research
19-Sep-79	16:40	J	K. C. Balcomb, The Center for Whale Research
23-Sep-79	11:21	J, K	K. C. Balcomb, The Center for Whale Research
29-Sep-79	17:45	L	R. Osborne, The Whale Museum
7-Jul-80	15:30	J	R. Osborne, The Whale Museum
19-Jul-80	11:50	J	R. Osborne, The Whale Museum
30-Jul-80	17:50	J	R. Osborne, The Whale Museum
11-Aug-80	10:53	K	R. Osborne, The Whale Museum
14-Aug-80	13:00	L	R. Osborne, The Whale Museum
16-Aug-80	19:15	J	R. Osborne, The Whale Museum
30-Aug-80	19:25	J, K, L	R. Osborne, The Whale Museum
9-Sep-80	3:47	J, K, L	R. Osborne, The Whale Museum
12-Sep-80	13:45	J	R. Osborne, The Whale Museum
16-Sep-80	19:15	J	R. Osborne, The Whale Museum
19-Sep-80	9:51	L	R. Osborne, The Whale Museum
29-Sep-80	19:23	L	R. Osborne, The Whale Museum
4-Oct-80	7:08	K	R. Osborne, The Whale Museum
7-Dec-80	8:50	J, K	R. Osborne, The Whale Museum
22-Jun-81		J	R. Osborne, The Whale Museum
24-Jun-81		J	R. Osborne, The Whale Museum
24-Jun-81		J	R. Osborne, The Whale Museum
28-Jun-81	13:00	K	K. C. Balcomb, The Center for Whale Research
4-Aug-81	18:50	J, K	K. C. Balcomb, The Center for Whale Research
6-Aug-81	20:03	J, K, L	K. C. Balcomb, The Center for Whale Research
24-Aug-81	12:34	J, K, L	K. C. Balcomb, The Center for Whale Research
24-Aug-81	15:02	J, K, L	K. C. Balcomb, The Center for Whale Research
13-Aug-82	15:09	J, K	R. Osborne, The Whale Museum
16-Aug-82	9:41	J, K	R. Osborne, The Whale Museum
16-Aug-82	14:41	J, K	R. Osborne, The Whale Museum
23-Aug-82	16:00	J, K	R. Osborne, The Whale Museum
27-Aug-82	10:00	J, K	R. Osborne, The Whale Museum
27-Aug-82	20:26	J, K	R. Osborne, The Whale Museum
28-Aug-82	11:56	J, K	R. Osborne, The Whale Museum
28-Aug-82	12:37	J, K	R. Osborne, The Whale Museum
9-Sep-82	14:25	K	R. Osborne, The Whale Museum
7-Sep-83	17:28	K	R. Osborne, The Whale Museum
24-Jul-84	1723	K	R. Osborne, The Whale Museum
22-Sep-84	14:20	K	R. Osborne, The Whale Museum
22-Sep-84	15:05	K	R. Osborne, The Whale Museum
20-Oct-84	18:07	K	R. Osborne, The Whale Museum
25-May-85		J	K. C. Balcomb, The Center for Whale Research
28-May-85	3:30	J	K. C. Balcomb, The Center for Whale Research

5-Jun-85	9:29	J	K. C. Balcomb, The Center for Whale Research
22-Jun-85	13:26	K	K. C. Balcomb, The Center for Whale Research
24-Sep-89	15:42	J, K	R. Osborne, The Whale Museum
13-Jul-90	1519	K, L	R. Osborne, The Whale Museum
13-Jul-90		K, L	R. Osborne, The Whale Museum
4-Aug-90		K	K. C. Balcomb, The Center for Whale Research
25-Aug-90		J, K, L	K. C. Balcomb, The Center for Whale Research
2-Sep-90		J, K	K. C. Balcomb, The Center for Whale Research
9-Sep-90		J	K. C. Balcomb, The Center for Whale Research
18-Sep-90		J	K. C. Balcomb, The Center for Whale Research
20-Sep-90		L	K. C. Balcomb, The Center for Whale Research
13-Jun-91		J, K	K. C. Balcomb, The Center for Whale Research
24-Jun-91		J, K	K. C. Balcomb, The Center for Whale Research
25-Jun-91	8:45	J, K	K. C. Balcomb, The Center for Whale Research
3-Jul-91	22:00	J, K	K. C. Balcomb, The Center for Whale Research
8-Jul-91		K	K. C. Balcomb, The Center for Whale Research
16-Jul-91	23:25	K, L	K. C. Balcomb, The Center for Whale Research
26-Jul-91	14:45	J, K ,L	K. C. Balcomb, The Center for Whale Research
26-Jul-91	20:40	J, L	K. C. Balcomb, The Center for Whale Research
9-Aug-91		J, K	K. C. Balcomb, The Center for Whale Research
18-Aug-91		J, K	K. C. Balcomb, The Center for Whale Research
19-Aug-91		J, K	R. Osborne, The Whale Museum
22-Aug-91		J, K	K. C. Balcomb, The Center for Whale Research
26-Aug-91		J, K	K. C. Balcomb, The Center for Whale Research
29-Aug-91	21:15	J	K. C. Balcomb, The Center for Whale Research
2-Nov-91		J	K. C. Balcomb, The Center for Whale Research
8-Jul-92		J, K, L	K. C. Balcomb, The Center for Whale Research
8-Jul-92	11:35	J, K, L	R. Osborne, The Whale Museum
8-Jul-92	11:35	J, K, L	R. Osborne, The Whale Museum
8-Jul-92	11:35	J, K, L	R. Osborne, The Whale Museum
8-Jul-92		J, K, L	K. C. Balcomb, The Center for Whale Research
16-Jul-92		J, K, L	R. Osborne, The Whale Museum
19-Jul-92	23:20	J, L	K. C. Balcomb, The Center for Whale Research
25-Jul-92	13:26	J	R. Osborne, The Whale Museum
25-Jul-92	13:26	J	R. Osborne, The Whale Museum
27-Jul-92	14:25	L	R. Osborne, The Whale Museum
9-Aug-92	10:20	J, K, L	R. Osborne, The Whale Museum
9-Aug-92	10:43	J, K, L	R. Osborne, The Whale Museum
9-Aug-92	13:05	L	R. Osborne, The Whale Museum
22-Sep-92		L	K. C. Balcomb, The Center for Whale Research
11-Jun-97		K	K. C. Balcomb, The Center for Whale Research
27-Jul-97	5:28	K	K. C. Balcomb, The Center for Whale Research
10-Nov-97		L	K. C. Balcomb, The Center for Whale Research
27-May-98		K, L	K. C. Balcomb, The Center for Whale Research

1-Jun-01	7:23	K, L	Sea Sound Network Array, Lime Kiln Lighthouse
5-Jun-01	16:51	K	Sea Sound Network Array, Lime Kiln Lighthouse
7-Jun-01	9:24	L	Sea Sound Network Array, Lime Kiln Lighthouse
8-Jun-01	15:25	L	Sea Sound Network Array, Lime Kiln Lighthouse
15-Jun-01	12:29	K	Sea Sound Network Array, Lime Kiln Lighthouse
15-Jun-01	16:00	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
15-Jun-01	20:05	K	Sea Sound Network Array, Lime Kiln Lighthouse
16-Jun-01	11:24	K	Sea Sound Network Array, Lime Kiln Lighthouse
16-Jun-01	12:17	K	Sea Sound Network Array, Lime Kiln Lighthouse
16-Jun-01	14:09	K	Sea Sound Network Array, Lime Kiln Lighthouse
18-Jun-01	10:53	K	Sea Sound Network Array, Lime Kiln Lighthouse
19-Jun-01	12:56	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
19-Jun-01	19:41	J	Sea Sound Network Array, Lime Kiln Lighthouse
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20-Jun-01	17:02	L	Sea Sound Network Array, Lime Kiln Lighthouse
20-Jun-01	17:35	L	Sea Sound Network Array, Lime Kiln Lighthouse
21-Jun-01	9:46	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
21-Jun-01	15:24	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
21-Jun-01	17:25	K	Sea Sound Network Array, Lime Kiln Lighthouse
21-Jun-01	19:30	K	Sea Sound Network Array, Lime Kiln Lighthouse
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23-Jun-01	20:40	L	Sea Sound Network Array, Lime Kiln Lighthouse
24-Jun-01	9:49	K, L	Sea Sound Network Array, Lime Kiln Lighthouse
24-Jun-01	12:21	J, L	Sea Sound Network Array, Lime Kiln Lighthouse
24-Jun-01	13:01	J, L	Sea Sound Network Array, Lime Kiln Lighthouse
25-Jun-01	16:37	L	Sea Sound Network Array, Lime Kiln Lighthouse
26-Jun-01	18:21	K	Sea Sound Network Array, Lime Kiln Lighthouse
27-Jun-01	16:16	K, L	Sea Sound Network Array, Lime Kiln Lighthouse
28-Jun-01	13:54	K	Sea Sound Network Array, Lime Kiln Lighthouse
29-Jun-01	20:20	L	Sea Sound Network Array, Lime Kiln Lighthouse
29-Jun-01	20:35	L	Sea Sound Network Array, Lime Kiln Lighthouse
30-Jun-01	16:04	L	Sea Sound Network Array, Lime Kiln Lighthouse
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2-Jul-01	17:51	J	Sea Sound Network Array, Lime Kiln Lighthouse
3-Jul-01	16:46	K	Sea Sound Network Array, Lime Kiln Lighthouse
4-Jul-01	9:46	K	Sea Sound Network Array, Lime Kiln Lighthouse
4-Jul-01	11:18	K, L	Sea Sound Network Array, Lime Kiln Lighthouse
5-Jul-01	16:26	L	Sea Sound Network Array, Lime Kiln Lighthouse
12-Jul-01	17:23	K, L	Sea Sound Network Array, Lime Kiln Lighthouse
13-Jul-01	14:49	L	Sea Sound Network Array, Lime Kiln Lighthouse
14-Jul-01	9:00	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
14-Jul-01	13:51	J, K	Sea Sound Network Array, Lime Kiln Lighthouse

14-Jul-01	16:07	L	Sea Sound Network Array, Lime Kiln Lighthouse
17-Jul-01	12:30	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
17-Jul-01	17:43	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
19-Jul-01	9:50	K	Sea Sound Network Array, Lime Kiln Lighthouse
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4-Aug-01	13:35	J, L	Sea Sound Network Array, Lime Kiln Lighthouse
1-Sep-01	11:30	K	Sea Sound Network Array, Lime Kiln Lighthouse
22-Sep-01	12:37	L	Sea Sound Network Array, Lime Kiln Lighthouse
22-Sep-01	13:25	L	Sea Sound Network Array, Lime Kiln Lighthouse
3-Nov-01	13:33	J	Sea Sound Network Array, Lime Kiln Lighthouse
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16-Mar-02	11:23	L	Sea Sound Network Array, Lime Kiln Lighthouse
20-May-02	8:27	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
27-May-02	10:08	J	Sea Sound Network Array, Lime Kiln Lighthouse
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7-Aug-02	11:57	L	Sea Sound Network Array, Lime Kiln Lighthouse
11-Nov-02	16:42	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
16-Dec-02	10:40	L	Sea Sound Network Array, Lime Kiln Lighthouse
19-Apr-03	16:04	J	Sea Sound Network Array, Lime Kiln Lighthouse
22-Apr-03	8:17	J	Sea Sound Network Array, Lime Kiln Lighthouse
22-Apr-03	10:17	J	Sea Sound Network Array, Lime Kiln Lighthouse
22-Apr-03	12:14	J	Sea Sound Network Array, Lime Kiln Lighthouse
30-Apr-03	11:55	J	Sea Sound Network Array, Lime Kiln Lighthouse
3-May-03	18:24	J	Sea Sound Network Array, Lime Kiln Lighthouse
9-May-03	8:10	J	Sea Sound Network Array, Lime Kiln Lighthouse
10-May-03	6:37	J	Sea Sound Network Array, Lime Kiln Lighthouse
11-May-03	9:30	J	Sea Sound Network Array, Lime Kiln Lighthouse
11-May-03	12:20	J	Sea Sound Network Array, Lime Kiln Lighthouse
14-May-03	8:18	J	Sea Sound Network Array, Lime Kiln Lighthouse
14-May-03	8:25	J	Sea Sound Network Array, Lime Kiln Lighthouse
14-May-03	9:53	J	Sea Sound Network Array, Lime Kiln Lighthouse
14-May-03	9:57	J	Sea Sound Network Array, Lime Kiln Lighthouse
15-May-03	1300	J	Sea Sound Network Array, Lime Kiln Lighthouse
21-May-03	14:49	J	Sea Sound Network Array, Lime Kiln Lighthouse

22-May-03	13:25	J	Sea Sound Network Array, Lime Kiln Lighthouse
30-May-03	1539	J	Sea Sound Network Array, Lime Kiln Lighthouse
31-May-03	1038	J	Sea Sound Network Array, Lime Kiln Lighthouse
31-May-03	1139	J	Sea Sound Network Array, Lime Kiln Lighthouse
31-May-03	1249	J	Sea Sound Network Array, Lime Kiln Lighthouse
1-Jun-03	14:13	J	Sea Sound Network Array, Lime Kiln Lighthouse
9-Jun-03	1548	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
10-Jun-03	12:32	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
12-Jun-03	12:16	L	Sea Sound Network Array, Lime Kiln Lighthouse
13-Jun-03	1109	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
13-Jun-03	1202	L	Sea Sound Network Array, Lime Kiln Lighthouse
14-Jun-03	1615	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
16-Jun-03	1226	J	Sea Sound Network Array, Lime Kiln Lighthouse
17-Jun-03	1510	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
17-Jun-03	1649	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
17-Jun-03	1742	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
20-Jun-03	6:45	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
21-Jun-03	8:41	L	Sea Sound Network Array, Lime Kiln Lighthouse
21-Jun-03	14:10	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
21-Jun-03	1921	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
24-Jun-03	10:31	Js & Ks	Sea Sound Network Array, Lime Kiln Lighthouse
25-Jun-03	11:40	L	Sea Sound Network Array, Lime Kiln Lighthouse
25-Jun-03	15:25	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
25-Jun-03	15:35	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
26-Jun-03	8:08	K	Sea Sound Network Array, Lime Kiln Lighthouse
26-Jun-03	11:57	L	Sea Sound Network Array, Lime Kiln Lighthouse
26-Jun-03	17:04	L	Sea Sound Network Array, Lime Kiln Lighthouse
26-Jun-03	18:52	J, L	Sea Sound Network Array, Lime Kiln Lighthouse
27-Jun-03	12:37	K	Sea Sound Network Array, Lime Kiln Lighthouse
27-Jun-03	15:22	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
28-Jun-03	11:31	K	Sea Sound Network Array, Lime Kiln Lighthouse
29-Jun-03	13:25	L	Sea Sound Network Array, Lime Kiln Lighthouse
30-Jun-03	11:24	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
1-Jul-03	9:53	K	Sea Sound Network Array, Lime Kiln Lighthouse
2-Jul-03	17:27	K, L	Sea Sound Network Array, Lime Kiln Lighthouse
3-Jul-03	11:26	K, L	Sea Sound Network Array, Lime Kiln Lighthouse
3-Jul-03	13:32	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
3-Jul-03	20:09	J, K, L	Sea Sound Network Array, Lime Kiln Lighthouse
8-Jul-03	8:41	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
8-Jul-03	9:43	L	Sea Sound Network Array, Lime Kiln Lighthouse
8-Jul-03	9:51	L	Sea Sound Network Array, Lime Kiln Lighthouse
8-Jul-03	10:18	L	Sea Sound Network Array, Lime Kiln Lighthouse
8-Jul-03	15:53	L	Sea Sound Network Array, Lime Kiln Lighthouse
11-Jul-03	15:15	J	Sea Sound Network Array, Lime Kiln Lighthouse

12-Jul-03	11:20	J	Sea Sound Network Array, Lime Kiln Lighthouse
14-Jul-03	11:14	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
17-Jul-03	17:21	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
22-Jul-03	11:06	J, K	Sea Sound Network Array, Lime Kiln Lighthouse
28-Sep-79	21:55	WCT	K. C. Balcomb, The Center for Whale Research
30-Sep-80	23:19	WCT	R. Osborne, The Whale Museum
8-Oct-80		WCT	R. Osborne, The Whale Museum
9-Oct-80	3:09	WCT	R. Osborne, The Whale Museum
29-Sep-82	17:39	WCT	R. Osborne, The Whale Museum
2004		WCT	R. Bates, MMRG
11-Mar-04	20:44	Offshores	P. Spong, Orcalab
12-Mar-04	16:51	Offshores	P. Spong, Orcalab
18-Mar-04	3:40	Offshores	P. Spong, Orcalab
14-Mar-04	1:12	L98	P. Spong, Orcalab
24-Mar-04	16:35	L98	P. Spong, Orcalab
26-Mar-04	5:25	L98	P. Spong, Orcalab
26-Mar-04	20:11	L98	P. Spong, Orcalab
27-Mar-04	19:30	L98	P. Spong, Orcalab
27-Mar-04	20:22	L98	P. Spong, Orcalab
13-Jul-02	2 sessions	A73	P. Spong, Orcalab
14-Jul-02	2 sessions	A73	P. Spong, Orcalab

Soundfiles of individual calls recorded from L98 between 25-Sept-03 and 13-Oct-03 were classified and provided by R. Griffin. Call type classification was confirmed by the author.

Appendix iv

A short note on the fundamental frequency of the primary call type from a resident, transient and offshore pod.

This work was considered too preliminary to be included in chapter 6 as I analysed only one focal call type for each ecotype and I was unable to expand upon it in the time frame of this thesis. However I have included it as a short note in the appendices in the hope that it might initiate further research in this area.

Recordings were made on equipment with a flat response between 0.10 and 10 kHz Digitisation and call categorisation were carried out using the same methodology as chapter 2.

I compared proportional usage of call types by group and selected the most common call of each ecotype for structural comparison. The N4 is the primary call type of the Northern Resident A4 pod and represented over 40% of the proportional call usage (Ford 1984). I randomly selected 30 samples of the N4 call type from 3 recordings sessions totalling 51 minutes of an isolated individual Northern Resident, A4 pod whale (A73) from July 2002.

There is a large amount of between and within regional variation in the proportional usage of call types amongst the West Coast Transients (Deecke 2003). In my recordings, (3 recording sessions, 189 minutes, 486 calls, 3 call types), the T7 call type (WCT07 Deecke 2003) was the primary call type, representing 69% of the call usage. I randomly selected 30 samples of the T7 call type from the 3 recordings sessions of West Coast Transients recorded between 1979-1980.

I analysed 89 minutes from three recordings sessions of Offshore killer whales from 2004 and identified and categorised 187 calls into 7 call types (see appendix ii), the primary call represented 28% of the proportional call usage and I randomly selected 30 samples of this call type for further analysis.

Using the measurement panel in Canary 1.2.4 software I was able to measure frequency parameters to a resolution of 0.01 kHz and duration parameters to 0.01 seconds. I measured the maximum and minimum frequency of the fundamental, the percentage of the fundamental between 0-0.5 kHz, 0.5-1.0 kHz, 1.0-2.0 kHz and >2 kHz. I also measured the frequency of the peak energy of the spectra of the call.

As the distribution of some measurements was skewed I compared mean values with Mann-Whitney U-tests. I also compared the variance of duration and maximum and minimum frequency measurements between ecotypes using Bartlett's test of homogeneity of variances.

Results

I found that the fundamental of the offshore call type was significantly higher in pitch then either the transient or resident call types (see table 1; figure 2). The fundamental of the resident call was also significantly higher in pitch than the transient call (see table 1; figure 2).

Maximum fundamental frequency:

offshore ($n = 26$) v resident ($n = 30$), $z = 6.407$, $p < 0.0001$

offshore ($n = 26$) v transient ($n = 28$), $z = 6.302$, $p < 0.0001$

resident ($n = 30$) v transient (28), $z = 6.535$, $p < 0.0001$

Minimum fundamental frequency:

offshore ($n = 26$) v resident ($n = 30$), $z = 6.317$, $p < 0.0001$

offshore ($n = 26$) v transient ($n = 30$), $z = 6.457$, $p < 0.0001$

resident ($n = 30$) v transient (30), $z = 6.708$, $p < 0.0001$`

% >2 kHz:

offshore (n = 24) v resident (n = 29), z = 6.218, p < 0.0001

offshore (n = 24) v transient (n = 25), z = 6.000, p < 0.0001

% 0-0.5 kHz:

resident (n = 29) v transient (n = 25), z = 6.289, p < 0.0001

% 1-2 kHz:

resident (n = 29) v transient (n = 25), z = 6.289, p < 0.0001

However there was no significant difference in the frequency of the spectral peak between the offshore and resident call types. The other comparisons of spectral peak were significant (see table 1; figure 2). Both the transient and resident call types had a higher mean spectral peak than mean maximum fundamental frequency suggesting that there is often higher energy in the harmonics than in the fundamental (see figure 2). This was not the case for the offshore call type. Pulsed call types often have more energy in the harmonics than the fundamental, but the fundamental nearly always has more energy in pure tones.

Spectral peak:

offshore (n = 26) v resident (n = 30), z = 1.15, p = 0.25

offshore (n = 26) v transient (n = 30), z = 5.055, p < 0.0001

resident (n = 30) v transient (n = 30), z = 5.22, p < 0.0001

There was a significant level of heterogeneity of variances between each ecotype for each of the three measurements compared. The variance was less for frequency measures than for duration consistent with previous studies except in the offshore call type. The offshore call had the greatest variance for all measures and the transient the least for all measures. The transient primary call type had significantly less variation in both frequency and duration variables than either the resident or offshore primary call type. Structural variation of a species' vocalisations can be caused by group and individual differences or contextual cues (Rendell et al. 1999) or due to structural change over time (Deecke et al. 2000). Individual and group differences in within-call type structure have been found in both resident and transient killer whale call type structure (Hoelzel and Osborne 1986; Saulitis 1993; Miller and Bain 2000; Nousek 2004). However my resident call type samples came from an isolated individual killer whale recorded within a two-day period. Residents call across most behavioural contexts (Ford 1984; 1989; Hoelzel and Osborne 1986; Morton 1990), transients calling is almost entirely limited to two contexts; following a kill and during social behaviour (Morton 1990; Saulitis 1993; Deecke et al. 2005). Variation in transient killer whale call types may be less due to the limited contexts in which transients call. Transients and residents both had less variance in the frequency variables than the duration, which is consistent with previous studies (Ford 1987; Saulitis 1993; Miller and Bain 2000). However the offshore call had greater variance in both frequency variables than the duration. I could not obtain sufficient temporal resolution to identify if this call was produced by rapid pulses or was a continuous tone, however qualitatively it appeared to be tonal. The tonal signature whistles of bottlenose dolphins often vary in pitch, but are easily recognisable by their distinctive frequency modulation contours (Caldwell et al. 1991). Offshore killer whale calls may be similarly flexible in pitch.

Maximum fundamental frequency:

$\chi^2_2 = 154.8$, $p < 0.0001$

Minimum fundamental frequency:

$\chi^2_2 = 42.7$, $p < 0.0001$

Duration:

$\chi^2_2 = 29.6$, $p < 0.0001$

Maximum fundamental frequency:

Transient var = 0.002, Resident var = 0.12, Offshore var = 0.199

Minimum fundamental frequency:

Transient var = 0.00, Resident var = 0.12, Offshore var = 0.105

Duration:

Transient var = 0.031, Resident var = 0.043, Offshore var = 0.050

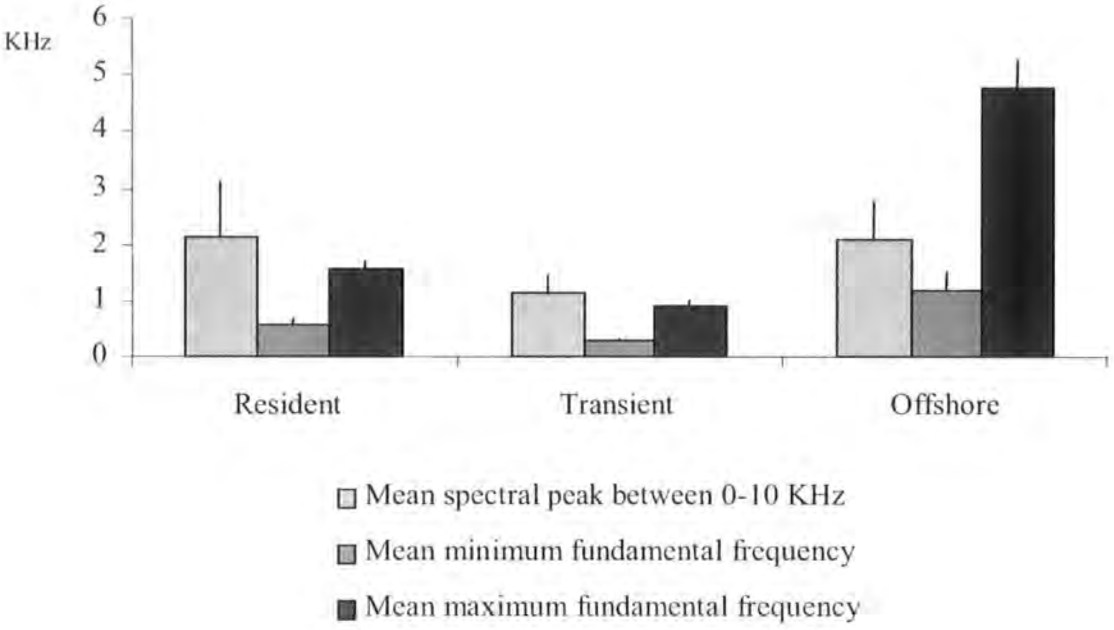
Table 1. Maximum and minimum fundamental frequencies and spectral peak between 0-10 kHz of the primary call of three different ecotype killer whale pods.

	Spectral peak between 0-10 kHz
Resident	mean = 2.1, s.d. = 1.0, range = 1.0 - 6.9
Transient	mean = 1.1, s.d. = 0.3, range = 0.9 - 2.2
Offshore	mean = 2.1, s.d. = 0.7, range = 0.9 - 3.4

	Minimum frequency
Resident	mean = 0.6, s.d. = 0.1, range = 0.3 - 0.8
Transient	mean = 0.3, s.d. = 0.02, range = 0.3 - 0.3
Offshore	mean = 1.2, s.d. = 0.3, range = 0.7 - 1.9

	Maximum frequency
Resident	mean = 1.6, s.d. = 0.1, range = 1.3 - 1.8
Transient	mean = 0.9, s.d. = 0.04, range = 0.7 - 1.0
Offshore	mean = 4.8, s.d. = 0.4, range = 3.8 - 5.4

Figure 2a. Maximum, minimum, peak spectral energy frequency and **b.** proportional frequency distribution of the fundamental frequency of the primary call types of three ecotypes.



e-mail: klohmann@email.unc.edu
†Department of Biology, University of Central Florida, Orlando, Florida 32816, USA

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Environment

Whale-call response to masking boat noise

Background noise can interfere with the detection and discrimination of crucial signals among members of a species. Here we investigate the vocal behaviour in the presence and absence of whale-watcher boat traffic of three social groups (pods) of killer whales (*Orcinus orca*) living in the nearshore waters of Washington state. We find longer call durations in the presence of boats for all three pods, but only in recent recordings made following a period of increasing boat traffic. This result indicates that these whales adjust their behaviour to compensate for anthropogenic noise once it reaches a threshold level.

Killer whales are the largest of the dolphin species and are highly social, living in matrifocal pods whose membership is stable over decades[1]. The vocal repertoire of whales in our study region shows pod-specific dialects, and there is a single primary call for each pod that represents up to 52% of the sounds produced by that pod[2].

Figure 1 Killer whales from the southern resident community in Washington state, pictured with onlookers.

We analysed the primary calls from each of the three pods that make up the collection of killer whales known as the southern resident community. Strategies that could be used by the whales to overcome interference from background noise include increasing the frequency, amplitude and duration of their signals. For example, humpback whales lengthen their song duration during playback of low-frequency active sonar[3]; and an improvement in perception threshold due to increased signal duration (in the context of the time required to integrate the signal) has been demonstrated in many species[4].

Today's southern resident population of killer whales is exposed to intense whale-watching activity (Fig. 1). This is associated with considerable boat engine noise — there is typically a fleet of 72 commercial vessels and an average of 22 boats following a pod during daylight hours. The number of boats has increased over the past decade and the population has been in decline since 1996 (Fig. 2). Southern resident killer whales may coordinate at least some aspects of cooperative foraging with their repertoire of discrete calls[2,5], and theoretical assessments[6,7] indicate that boat noise could impair communication between killer whales over a range of 1–14 km.

We compared recordings (for methods, see supplementary information) made in the presence or absence of boat noise during three time periods: 1977–81, 1989–92 and 2001–03 (some recordings provided by K. C. Balcomb). We found no significant difference in the duration of primary calls[2] in the presence or absence of boats for the first two periods, but a significant increase (about 15%) in call duration for all three pods in the presence of boats during the 2001–03 period (J pod: for t-test $t = 4.13$, for Mann–Whitney U-test $z = 4.09$, $P < 0.0001$, d.f. $= 134$; K pod: $t = 4.33$, $z = 3.36$, $P < 0.0008$, d.f. $= 162$; L pod: $t = 3.14$, $z = 2.97$, $P < 0.005$, d.f. $= 192$; see Fig. 2).

All comparisons of call rate were non-significant (and data were not available for an assessment of call amplitude). Functional differences between the repetition rate of calls and their duration may explain the lack of correlation for repetition rate, although we have no direct evidence for this. The average number of vessels attending the whales increased roughly fivefold from 1990 to 2000, suggesting that there is a threshold level of disturbance beyond which 'anti-masking' behaviour, such as increased signal duration, begins.

Structural changes have been found previously in the songs of birds and humpback whales in environments altered by humans[3,8], but our findings show a response that seems to be initiated to counteract anthropogenic noise only once it reaches a critical level.

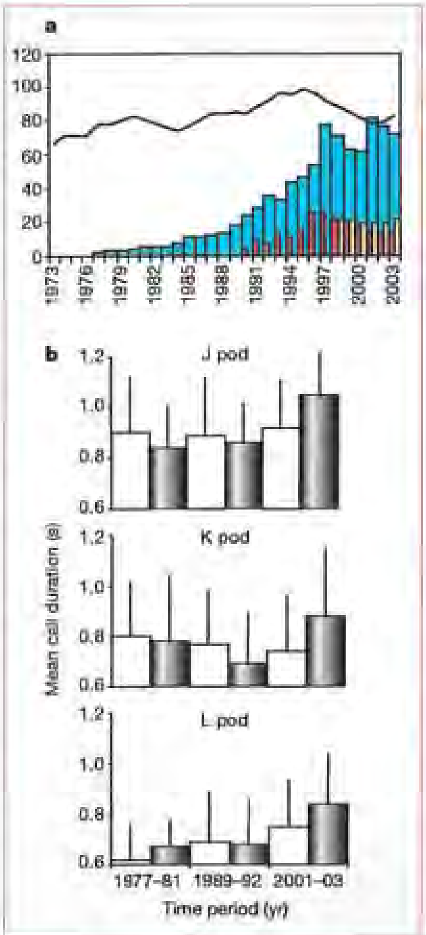

Figure 2 Effect of whale-watcher boat noise on calls made by killer whales. **a**, Boat and whale numbers are shown for the period between 1973 and 2003. Solid line, size of whale population; blue bars, number of active commercial boats per year; red bars, average number of boats following whales, measured from shore base (Lime Kiln Lighthouse, San Juan Island, Washington state; data for 1990–2003 only); yellow bars, average number of vessels following whales, measured using boat-based observations (1998–2003 only). **b**, Call duration in seconds for the three pods (termed J, K and L) recorded in the presence (black) and absence (white) of boats for each time period (error bars show 1 s.d.).

Andrew D. Foote*, Richard W. Osborne†, A. Rus Hoelzel*
**School of Biological and Biomedical Sciences, University of Durham, Durham DH1 3LE, UK*
e-mail: a.r.hoelzel@dur.ac.uk
†The Whale Museum, PO Box 945, Friday Harbor, Washington 98250, USA

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